

QUANTITATIVE STUDIES ON SPERMATOGENESIS IN THE ALBINO RAT

III. VOLUME CHANGES IN THE CELLS OF THE SEMINIFEROUS TUBULES¹

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FOUR FIGURES

Since 1950 several authors have published quantitative studies on normal spermatogenesis of the rat. These studies established the number and mode of spermatogonial mitoses (Roosen-Runge and Giesel, '50; Clermont and Leblond, '53), criteria for stages of the spermatogenic cycle and periodic changes in the shape of the Sertoli cell nuclei (Leblond and Clermont, '52a, '52b), and the numbers of germ cells and Sertoli cells (Roosen-Runge, '54a, '54b). In addition, an estimate of the duration of spermatogenesis (Roosen-Runge, '51) and data on the degeneration of germ cells during normal spermatogenesis (Roosen-Runge, '54a) were obtained. But our knowledge of multiplication rates and of the structure of cells at different stages of normal spermatogenesis do not yet suffice to explain the regulatory mechanisms involved in this process. For further exploration of the growth of germ cells Chalkley's ('43) method of determining the volume of tissue components seemed to offer promise and at the same time to permit a study of the volume of Sertoli cells throughout the spermatogenic cycle.

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MATERIAL AND METHODS²

All counts reported in this paper were made on one testis of a healthy Sprague-Dawley rat weighing about 350 gm. Confirmatory material relating to volume changes in seminiferous tubules was obtained from two other rats. The testes were fixed by injection of Stieve's solution into the testicular artery. Paraffin sections of 8μ thickness were made and stained with PAS technique and acid hemalum.

Determination of tubular volume. Diameters of sections of tubules were measured on photographic prints at a magnification of $72\times$ by means of a watchmakers caliper with vernier scale. In the case of ellipsoidal sections the principal minor axis was measured. Only those sections were disregarded which appeared to miss the center of the tubule. In 5 different sections, at least 1 mm apart from each other, 929 sections of tubules were measured. Volumes in μ^3 per cm of length of tubule were calculated from the diameters. It was felt that the problem of shrinkage through fixation and embedding does not enter into the present study which is concerned with the relative volumes of fixed tubules and cells.

Determination of relative cell volumes. The method used was initiated by Chalkley in 1943. It has since been explored by several authors, notably Eschenbrenner, Miller and Lorenz ('48), who used it for an histological analysis of the effect of chronic whole body irradiation on the testicular tissues of mice. The method was recently discussed in some detail by Roosen-Runge ('54c) in connection with quantitative studies on the human testis. An eyepiece was fitted with 5 pointers. Four were used for recording and a short 5th one for focusing. Focusing on a field with an oil immersion objective, the structures at the tips of the 4 main pointers were recorded as "hits." The field was then thrown out of focus, the stage moved a little along a zig-zag course through the preparation, a new structure brought into focus under the short pointer,

² The assistance of Miss Joyce Stratford who made all counts and measurements is gratefully acknowledged.

and the procedure repeated. After several thousand such determinations the relative frequency of the "hits" on any particular type of cell or other structure indicates the relative volume occupied by all cells or structures of that type. The number of hits recorded on structures in the seminiferous tubules was 25,770. In the main series of counts, whenever a pointer indicated an extratubular structure (outside the basement membrane) no hit was counted. If a structure could not be satisfactorily identified it was recorded as "space." In a smaller series of measurements only hits on Leydig cells, interstitial space and seminiferous tubules as such were recorded.

An essential prerequisite for the successful use of Chalkley's method is accurate and consistent identification of items to be recorded. The criteria used in identifying the stages of spermatogenesis and the components of the seminiferous tubules as defined for the purpose of the present paper are described in the following paragraphs.

Definition of stages of spermatogenesis. In previous studies a division of spermatogenesis into 8 stages was used (Roosen-Runge and Giesel, '50). This classification had two major advantages: it was readily correlated with some older work in the field and its first stage coincided with the actual beginning of spermatogenesis, i.e. with the first spermatogonial divisions. Leblond and Clermont ('52a) defined 14 stages of spermatogenesis by means of cytological features in the developing spermatid as demonstrated by the PAS technique. Although their stages would seem to be the most clearly defined in the literature, Leblond's and Clermont's classification has some disadvantages which made it unsuitable for the purposes of this investigation: Their stage I begins with the early spermatid rather than with the early spermatogonium, and the stages are entirely based on minute changes in the spermatid cell. In addition, it was considered advisable to use a lesser number of stages. Our own classification was, therefore, used again, but some small changes were introduced in order to improve the definitions of the stages and to

permit closer correlation of several stage limits with corresponding ones of Leblond and Clermont. The most important change was the use of the PAS stain as a tool in identification. This was applied specifically in order to define the limits of stages V and VI. The flattening of the PAS stained acrosome onto the nucleus was chosen as the criterion for the beginning of stage VI. Roman numerals were chosen to conform to Leblond's and Clermont's terminology. (For a comparison between our classification and that of Leblond and Clermont see figure 1, for a tabulation of other classifications see Leblond and Clermont, '52a, table 1).

Definition and identification of components of the seminiferous tubules. Satisfactory identification of a cell is not

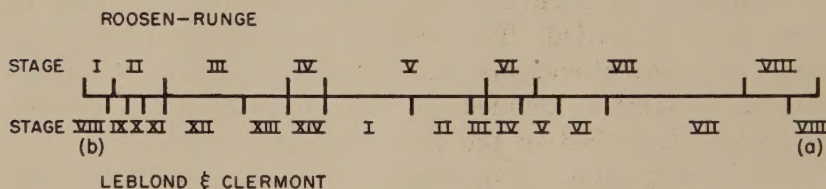


Fig. 1 Comparison of stages of spermatogenesis as used in the present paper with those of Leblond and Clermont ('52b). The relative lengths of the stages are approximations derived from the frequencies of occurrence of the stages. See text for stage definitions.

always possible when only a small fragment of the cell is visible in the plane of focus. With this in mind, the following paragraphs present the definitions used and the difficulties encountered in the practical identification of structures in our preparations.

Spermatogonium Type A. A cell at the basement membrane, with a pale, ovoid nucleus showing fine chromatin granules evenly distributed. The cell is present at all stages of the cycle. The nucleus is characteristic, but the cytoplasm stains faintly and the cell borders are tenuous. Identification may be difficult when the pointer is on the cytoplasm and the nucleus is not in the same plane.

Spermatogonium Type B. A cell at the basement membrane, with an ovoid to round nucleus showing coarse chromatin

bodies attached to the nuclear membrane. The cell is found with increasing frequency from stage V through stage VIII. It is easily identified as it has definite cell borders and relatively little cytoplasm, which in stages VII and VIII stains characteristically with PAS. Leblond and Clermont ('53) recognized an "intermediate type" of spermatogonium, which was not distinguished in the present investigation.

Spermatocyte. A cell, usually not in contact with the basement membrane. In contrast to the spermatogonium the nuclear membrane of the spermatocyte is poorly defined and typical chromatin configurations are found in the various stages of meiosis. In this study no distinction was made between primary and secondary spermatocytes.

Spermatid. The early spermatid has a spherical nucleus with small amounts of chromatin. Later the nucleus elongates and undergoes a series of characteristic transformations. The cytoplasm at first surrounds the nucleus but gradually elongates toward the lumen of the tubule. At this time the cytoplasm begins to stain lightly with PAS. The early spermatid from stage V to VIII is more easily identified than any other cell in the tubule.

Spermatozoon. The spermatid arises at the end of stage IV. After passing through a whole cycle and again entering stage V as a much more differentiated cell, it is now called a spermatozoon. According to this definition spermatozoa exist only in stages V to VIII. They are easily recognized by their heads and tails. Part of their cytoplasm is lost in the form of residual bodies from stage VII on.

Residual bodies. Bodies of varied sizes which stain darkly with hematoxylin and are located near the lumen in stages VII and VIII. In stage I they are found in lesser numbers and more peripherally, even at the basement membrane, and at this time they stain more or less with PAS while hematoxylin stains them lightly or not at all. In the present paper no evidence is brought forward that the bodies found in stage I are actually the same as those in stages VII and VIII.

Sertoli cell. This cell contains a characteristic nucleus which is peripherally located and has a large round nucleolus. Its cytoplasm contains varying amounts of PAS positive granules and is somewhat more dense than that of the surrounding spermatocytes and young spermatids. The bulk of its cytoplasm is easily identified in the peripheral part of the tubule, but in its central portions identification poses problems which will be presented in detail in the discussion.

Basement membrane. A nucleated layer, between 1 and 2μ thick, which surrounds the tubule and is strongly PAS positive.

Space. Whenever a structure under a pointer could not be satisfactorily identified it was recorded as "space." Occasionally this was an artifact in the tissue, but more often it was of a cytoplasmic nature.

The standard error of the mean may be used as an indication of the accuracy of identification. The standard error was determined for three cell types: the spermatogonia, which have little collective bulk and are consequently recorded with low frequency; the Sertoli cells which are more voluminous but present difficulties to the observer because of the elusiveness of their cytoplasmic processes; and the spermatids which occur with high frequency and can be easily identified. Table 1 shows that the per cent standard error varies from 38.8 for spermatogonia in stage IV to 1.5 for spermatids in stage VII. For the majority of items measured the standard error is below 10%.

RESULTS

Table 2 summarizes the crude data obtained by Chalkley's method. In figure 2 these data have been used to construct a graph which demonstrates the relative volume of each component of the tubule at each stage of spermatogenesis. The distribution of the stages along the time axis was determined in the following way: It was assumed that the relative frequency of tubular sections in any given stage is representative of the relative duration of that stage. However, the relative

TABLE 1

Relative volumes of spermatogonia, spermatids and Sertoli cells, and standard errors. (The mean volumes are expressed in per cent of the total volume of the tubule)

	SPERMATOGONIA		SPERMATIDS		SERTOLI CELLS	
	Volume	S.E.	Volume	S.E.	Volume	S.E.
Stage I	1.8	0.49	38.1	2.00	7.9	0.87
Stage II	0.5	0.15	39.0	1.04	9.0	0.60
Stage III	1.0	0.19	33.9	1.25	9.4	0.82
Stage IV	0.8	0.31	31.4	1.40	9.3	0.96
Stage V	1.3	0.21	28.9	0.83	9.3	0.35
Stage VI	1.3	0.24	29.7	0.88	8.0	0.49
Stage VII	2.7	0.15	30.0	0.46	10.0	0.36
Stage VIII	3.7	0.31	29.9	0.92	9.2	0.58

TABLE 2

Number of "hits" on components of seminiferous tubules in different stages of spermatogenesis

	STAGE								TOTAL "HITS"	% OF "HITS"
	I	II	III	IV	V	VI	VII	VIII		
Spermatogonia A	4	10	25	11	66	9	13	5	143	0.6
Spermatogonia B	21	0	0	0	10	20	189	87	327	1.3
Young spermatocytes	56	117	163	82	0	0	0	0	418	1.6
Older spermatocytes	286	493	685	417	414	184	935	379	3793	14.7
Spermatids	520	790	844	411	1822	690	2241	743	8061	31.2
Spermatozoa	0	0	0	0	1987	629	928	179	3723	14.4
Residual bodies	33	2	0	0	0	0	193	100	328	1.3
Abnormal germ cells	3	3	1	0	9	0	1	0	17	0.1
Sertoli cells	108	182	235	122	586	185	746	228	2392	9.3
Lumen	275	352	429	211	1127	513	1993	688	5588	21.6
Basement membrane	45	66	84	42	188	59	155	54	693	2.7
Space (un- knowns)	17	15	24	13	82	38	79	19	287	1.2
Total "hits" per stage	1368	2030	2490	1309	6291	2327	7473	2482	25770	
Per cent of all "hits"	5.3	7.7	9.9	5.1	24.4	9.0	29.0	9.6	100	

frequency of stages as given in table 2 depends in part on the volume of the tubule. It was, therefore, considered more reliable to use the data obtained in the course of the investigation of tubular diameters (table 3). The middle of each stage was calculated and converted into hours on the assumption

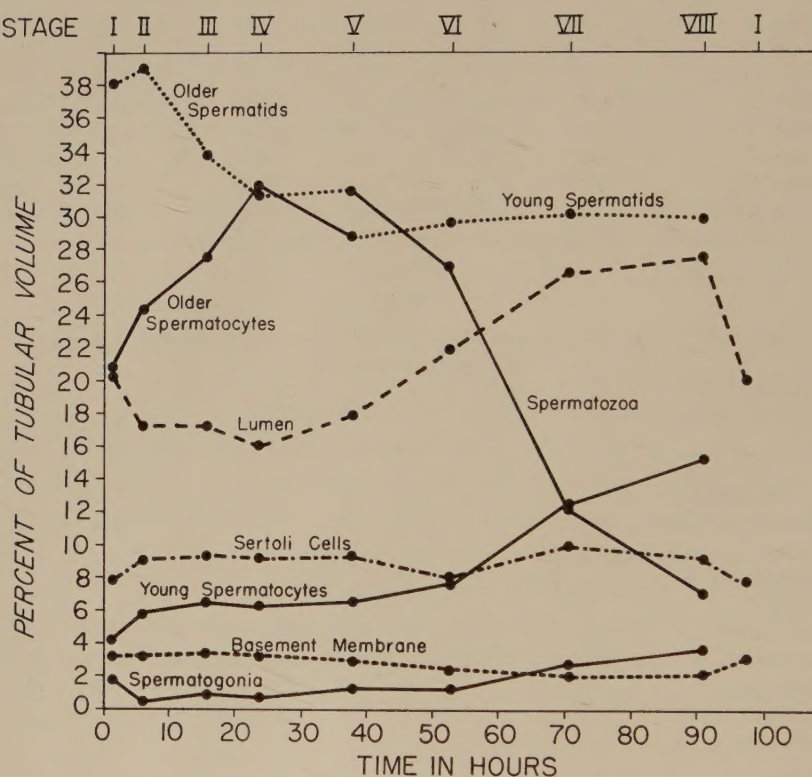


Fig. 2 Relative volumes of components of the seminiferous tubules of the rat at 8 stages of the spermatogenic cycle. See text for explanation of time scale.

tion that each spermatogenic cycle has a duration of approximately 4 days (Roosen-Runge, '51). It is obvious that the absolute time values in the figures are rough approximations.

Figure 3 shows the volume changes of the whole tubule and of several of its components throughout the cycle. The data were calculated from the values presented in tables 2

TABLE 3

Diameter and volume of seminiferous tubules in different stages of spermatogenesis

	NUMBER OF SECTIONS	MEAN DIAMETER IN μ	S.D.	RANGE IN μ	VOLUME/CM IN $10^3 \mu^3$
Stage I	30	211.8	23.2	207-250	3.50
Stage II	82	216.3	20.4	178-288	3.67
Stage III	86	208.1	25.0	159-275	3.41
Stage IV	65	221.7	23.7	193-280	3.85
Stage V	212	227.9	26.1	184-304	4.07
Stage VI	75	228.2	25.3	165-311	4.10
Stage VII	288	236.9	27.0	158-315	4.41
Stage VIII	91	241.9	31.3	201-321	4.60
Totals:	929	228.3		158-321	

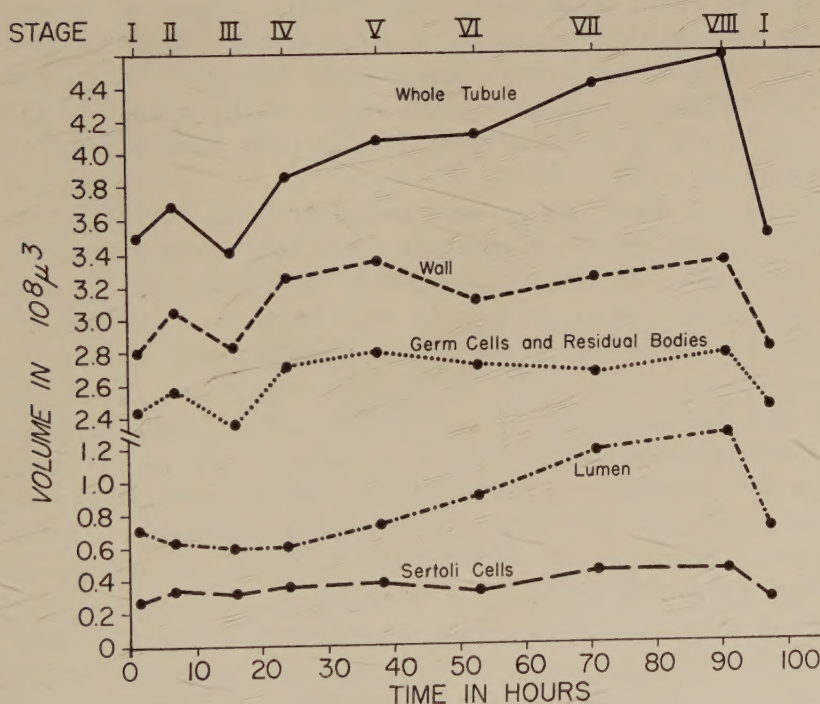


Fig. 3 Average absolute volumes of seminiferous tubules and some of their components, at 8 stages of the spermatogenic cycle. See text for explanation of time scale.

and 3. These data were confirmed by measuring 950 sections of tubules in two different rats. Essentially the same changes were found, i.e. the volume was in each case highest in stage VIII, dropped sharply in stage I, reached its lowest point in stage III and gradually increased through the succeeding stages. In figure 3 it is shown that the increase in tubular volume which occurs from stage V to stage VIII is due only to widening of the lumen and not to an increase in the bulk of the cellular components. On the other hand, changes in the tubular volume in stages I to IV are apparently due to changes in total germ cell volume with no accompanying changes in the width of the lumen.

The relative volume of interstitial tissue was determined in a separate series of 300 hits on testicular tissue in general and was found to be 9.7%. The relative volume of Leydig cells was calculated from the number of hits (295) recorded with 15,863 hits on tubular components. Knowing the volume of all tubular components to be 90.3% of the volume of the whole testis, it followed that Leydig cells have a relative volume of 1.7%.

Figure 4 shows the volume changes of the average individual germ cell as it matures from late spermatogonium to spermatozoon. Volume changes of the Sertoli cell are also represented. The graph must be regarded as a rough approximation because it is derived from a combination of data on relative cell volumes (fig. 3), absolute tubular volume (table 3) and cell numbers (Roosen-Runge, '54a). Cell numbers were established in this previous study by counts in whole mounts of tubules. It was found that a section of tubule of 1 cm length and 240μ diameter contained 13,800 Sertoli cells, 38,600 spermatogonia Type B and 34,100 spermatocytes in stage VIII, and 122,000 spermatozoa in stage VI. These figures were used to calculate the volumes of the individual cells from the data on relative total volumes of the corresponding cell kind. The graph suggests that the growth of the primary spermatocyte is approximately exponential and that it grows to about 7 times the volume of the late spermato-

gonium. The spermatid undergoes little volume change. The spermatozoon begins to lose bulk during stage V, at a time when there is still little visible evidence for a loss in cytoplasm. The Sertoli cell shows a cyclic change of volume. During stages VII and VIII the cell is at its largest, whereupon its bulk decreases rapidly by about 40% until the middle of stage I. The increase in volume from stage I to stage VII appears to be interrupted by a decrease during stage VI. The average size of the Sertoli cell appears to be nearly the same as that of the primary spermatocyte at its largest.

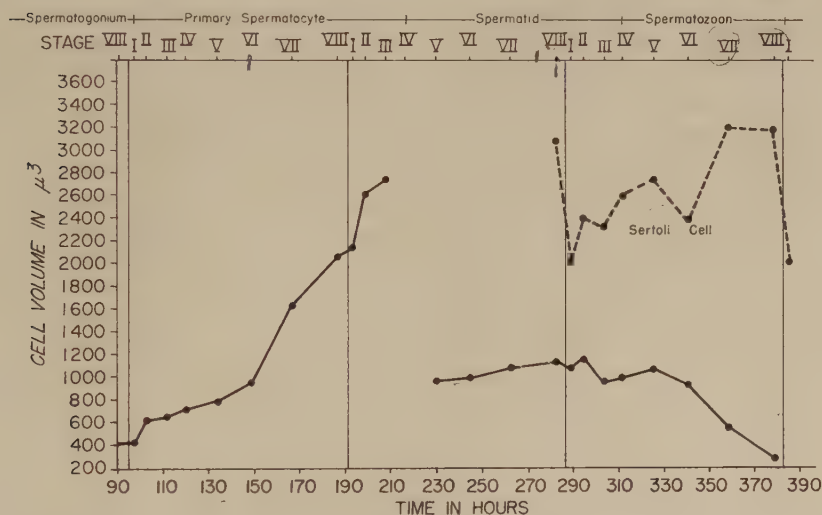


Fig. 4 Average volume of the Sertoli cell, and of the germ cell from late spermatogonium to spermatozoon. See text for explanation of time scale. The volume of the spermatocyte at stage IV is unknown, because the number of cells present during maturation divisions has not been determined.

DISCUSSION

The results concerning the volume changes in the Sertoli cell are not easily explained. Elftman ('50) has shown that the Sertoli cell in the mouse undergoes conspicuous changes in shape particularly during the stages immediately following the departure of the spermatozoa from the tubule. Leblond and Clermont ('52a) demonstrated that at the corresponding

stages in the rat there is a decrease in the frequency of those nuclear forms which indicate elongate and narrow Sertoli columns, and an increase in the forms which are representative of short cells more or less retracted toward the basement membrane. In the present investigation a very significant loss of cell volume was found to occur at the same stage.

The question arose whether the results obtained by Chalkley's method might have been distorted through an inability to identify fine ramifications of the Sertoli cell. The boundaries of the Sertoli cell in the rat are often difficult to ascertain. We have not yet found a method which demonstrates fine ramifications—if they exist—in the same unequivocal way in which Elftman demonstrated them in the mouse (see his fig. 1). With the stains used in the present study no Sertoli cell cytoplasm could be discerned between the spermatids near the lumen and between the heads of the spermatozoa in stages VII and VIII. From analogy with the mouse and from established concepts it seems probable that very fine cytoplasmic processes are present, but their volume must be very small in comparison to the bulk of the Sertoli cells.³ It also seems probable that a minimum of ramification exists immediately after the departure of the spermatozoa and before the new generation of spermatids has become attached to the Sertoli cells. At this period, at which the greatest part of the cytoplasm should be easily identifiable, our data show the cell volume to be at a minimum. It is, therefore, probable that the decrease in volume from stage VIII to stage I is real and significant.

Van Oordt et al. ('54) have shown that in the frog testis large vacuoles at the base of the Sertoli cells increase in size until the final stages of sperm release, after which they apparently return to a minimal size. This cyclic behavior

³In electron micrographs of Fawcett and Burgos ('55) the Sertoli cell ramifications can be seen surrounding individual spermatids of cat and man. However, the extent of these ramifications is usually beyond the limit of resolution of the light microscope.

appears to be correlated with a fluid uptake by the tubule and specifically by the Sertoli cell. In the rat there is no vacuole which might be used as a convenient indicator of fluid exchange, but the analogy otherwise appears close. It is possible that the Sertoli cell takes in fluid slowly throughout the spermatogenic cycle until the final release of the spermatozoa when fluid is suddenly poured into the tubule. This may aid the transport as well as the release of the spermatozoa.

SUMMARY

Chalkley's method for determining the relative volume of tissue components in histological preparations was applied to the cells of the seminiferous tubules of the rat in 8 different stages of the spermatogenic cycle. The resulting data on relative cell volumes were combined with data on the numbers of cells in the tubules in calculating the approximate average volume of the individual germ cell at different phases of its life.

The growth of the primary spermatocyte is approximately exponential. This cell appears to have no decelerating growth phase before it enters the first meiotic division. The total increase in volume from late spermatogonium to spermatocyte just before the first maturation division is at least 7 fold.

The Sertoli cell undergoes cyclic volume changes, the most pronounced of which is the loss of about 40% of volume immediately after or during the release of the spermatozoa from the tubule.

The total volume of Leydig cells was determined in a separate series of counts and was found to be 1.7% of the total volume of the testis.

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THE FINE STRUCTURE OF YOUNG AND OLD SPINAL GANGLIA ¹

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SEVENTEEN FIGURES

Despite the intensive studies devoted to the structure of nerve cell bodies and the extracellular and intracellular elements associated with them, there are still many aspects of the structural organization of the cells of the spinal ganglia awaiting final resolution.

It has been suggested that there are various nerve cell types in spinal ganglia, and some authors have even assigned different functional properties to these cells based on a histological study of sections with the light microscope (see Bacsich and Wyburn, '53). The disposition of the Nissl bodies, mitochondria, and Golgi apparatus in these cells has occupied much attention (Beams, van Breemen, Newfang and Evans, '52). The satellite cells of the ganglion also have been investigated. In addition, the ageing of nerve cells and the accumulation of lipofuchsin pigment (Andrew, '52) has been observed frequently.

In this study of spinal ganglia, we have attempted, through the application of ultrathin sectioning and electron microscopy to:

(1) ascertain the possible occurrence of cell types and characterize morphologically the basis for any such cell variants;

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² With the technical assistance of Charles E. Houck, Jr. and Emil C. Sanders.

- (2) study the fine structure of the karyoplasm, nucleolus, and cytoplasm or neuropilasm;
- (3) resolve further the structure of Nissl bodies or chromophil substance;
- (4) determine the disposition and structure of mitochondria;
- (5) study the occurrence and structure of the Golgi apparatus;
- (6) study the morphology of the satellite cells and their relationship to the spinal ganglion nerve cells and to each other;
- (7) investigate in senile animals the spinal ganglion cells, their mitochondria and the distribution and fine structure of the pigment and to draw some conclusions as to the probable mechanism of its formation.

MATERIAL AND METHODS

The spinal ganglia of guinea pigs were used. The animals were divided roughly into three groups: (1) *young* animals of three days of age; (2) *adult* animals that had given birth to at least one litter; (3) *old* or *senile* animals of 6 years of age. These latter animals were donated generously by Dr. James B. Rogers of the Department of Anatomy, University of Louisville School of Medicine, Louisville, Kentucky, to whom we are very grateful.

The techniques were essentially the same as those used previously for the study of the fine structure of peripheral nerve fibers (Hess and Lansing, '53). The spinal ganglia, dissected most frequently from thoracic vertebral levels, were placed in Dalton's fixative (Dalton and Felix, '55) for one-half to two hours. Most of the sections examined were obtained from material allowed to fix for one and one-half hours. The ganglia then were washed in distilled water and placed in 70% alcohol, dehydrated and embedded in a mixture of partially polymerized butyl and methyl methacrylate. A few ganglia were also fixed in buffered osmic acid (Palade, '52a), varying in concentration from 1% to 3% and contain-

ing mammalian Ringer's solution, for 4 hours, then similarly treated as above. The fixation yielded by Dalton's fluid was vastly superior. Previous studies in this laboratory have shown that nerve tissue has a predilection to swell and "explode" during the embedding process. The use of partially polymerized plastic for embedding usually prevents this, although it does not invariably yield perfect results.

Sections were made and mounted on copper mesh grids, which were then inserted into an RCA-EMU type microscope. Negatives were exposed at a magnification of 1000 to 6000 $\times$ and photographically enlarged.

To facilitate identification of the cellular elements and to determine the location in the ganglia of the section under observation in the electron microscope, thin plastic sections were studied in the phase-contrast microscope. Reference was also made to cytological and neurohistological frozen and paraffin preparations of spinal ganglia to correlate observations made with the light and electron microscopes.

RESULTS

Spinal ganglion nerve cells

Cell types. In ganglia from guinea pigs of all ages, two distinct cell types are found (fig. 1). In one, the cells are small, the cytoplasm is very osmophilic, and the ground substance or neuroplasm of the cell is well organized; the chromophil substance extends evenly throughout the cell (fig. 15). In the other cell type, the cells are large, the intensity of osmophilia is low, the Nissl substance is easily recognized and organized into scattered clumps or bodies (fig. 7). That this is a real difference and is not necessarily a factor induced by fixation can be seen by observing these two cell variants in juxtaposition to one another. The main difference between these two cell types resides in the distribution of the Nissl substance, with the first or "dark" type of cell having chromophil substance extending throughout the length and breadth of the cell, thus giving high electron density to

the cytoplasm; while the second or "light" type of cell has Nissl substance distributed in discrete clumps and producing in general a low electron density of the cytoplasm.

There are transitional cell types with density of cytoplasm and of cytoplasmic elements ranging in intensity between the "dark" and "light" cell variants (fig. 1). However, the "dark" and "light" cell types as indicated above are representative of such a dichotomy in spinal ganglion nerve cells.

The remaining items will be discussed in relation to the cell types, and the differences, if any, in the morphology or disposition of the elements under consideration will be noted.

Nucleus and nucleolus. The nucleoplasm of spinal ganglion cells is sparse and irregularly dispersed (fig. 16). The nucleus possesses a typical double membrane (figs. 15 and 16). The nucleolus is very dense and consists of at least three components (fig. 16). One is a vesicular component with filaments enclosing small vacuoles and is the most prominent part of the nucleolus. Another portion of the nucleolus, most frequently intimately associated with the filamentous structure, is a dense irregular mass yielding mainly a homogeneous appearance with only a few large granules. Other irregular masses, presenting a more granular appearance than the former and less dense, comprise the third component of the nucleolus.

Any one of these three nucleolar components can be found adherent or closer to the nuclear membrane than the others (fig. 9), yielding an appearance similar to that of the nucleolar satellite (Barr, Bertram and Lindsay, '50); we have no information as to its significance.

There are no differences in the cell types of nucleus or nucleolus. The nucleolar satellite body also appears in both cell types.

Cell membrane. The limiting cell membrane of the spinal ganglion nerve cell presents a structure similar to the membranes of other cells. It is rather difficult to define its exact structure and dimensions since the satellite cell, to be discussed later, is in juxtaposition with it.

Most frequently, the nerve cell membrane is smooth. However, often it reveals thin villiform projections extending outward from the nerve cell surface (fig. 7). The margins of these processes are continuous with the cell membrane. The less dense central portion of these projections has the same density as the nerve cell cytoplasm, so that these villiform projections are true processes of the nerve cell. The projections are also seen cut in cross-section. They are probably due to the harsh treatment accorded the nerve cell by fixation.

Neurofibrils. We have seen no structure in the cytoplasm that can be interpreted as a neurofibril. Indeed, the opposite view is probably true in that there appears to be no orientation in the cytoplasm, either of the neuroplasm itself or of the distribution of the cytoplasmic elements, except for the internal organization of the Nissl substance discussed below. The fibrillar structures mentioned by Beams et al. ('52) as neurofibrils do not appear in our material.

Chromophil substance. The observation that Nissl bodies contain ribonucleoprotein suggests that this substance should appear morphologically similar to the structural system described as "endoplasmic reticulum" by Palade and Porter ('54), "ergastoplasm" by Weiss ('53), and double-membraned system by Weiss and Lansing ('53). Although none of these terms is entirely appropriate for nerve tissue, the term "ergastoplasm" will be used in this paper. The latter presumably corresponds to the basophilic material in cytoplasm (Bernhard, Haguenau, Gautier and Oberling, '52). Haguenau and Bernhard ('53) have described Nissl material in nerve cells with the use of the electron microscope.

When the Nissl substance is viewed under relatively low magnification, it appears as a densely-packed mass of small granules (figs. 7 and 15). However, with higher magnification, some of the granules can be resolved as very fine tubular filaments surrounded by granules (figs. 11 and 14). This is an appearance similar to endoplasmic reticulum or ergastoplasm previously described in nerve tissue (Hess and

Lansing, '53). The tubular filaments are in layers, one placed on top of the other. The granules are perhaps more numerous than those of ergastoplasm in other cells. At higher magnifications, the granules are seen to have smaller, denser granules in and around them, yielding a punctate appearance. In addition, the granules associated with the tubular filaments are usually not only aligned against the filaments, but also frequently can be found evenly-spaced in a row between the filaments. The tubular elements of each Nissl body are also highly oriented, so that in a mass of Nissl, all the components are sectioned in the same direction. One Nissl body may have its tubules cut neatly in cross-section; while in an adjacent clump of Nissl, all the units may be cut tangentially.

Clumps of Nissl substance appear only in "light" cells; aggregations occur throughout the cytoplasm of "dark" cells. However, even though the distribution of chromophil substance differs in the two cell types, the units composing the Nissl substance are the same (figs. 11 and 14).

Mitochondria. The mitochondria are small, thin, and elongated and possess the cristae or folds characteristic of this organelle (figs. 7, 11 and 15). They are, in principle, similar to mitochondria previously described (Palade, '52b; Hess and Lansing, '53). Higher magnifications reveal at times that the folds of mitochondria do not pass across the entire width of the mitochondrion, but are seen cut in cross-section (fig. 12). The haphazard arrangement of the folds in the interior of the mitochondrion indicate that perhaps the main folds possess villous extensions. Y-shaped and T-shaped bifurcating mitochondria have also been noticed.

One is impressed by the relatively small diameter of several of the mitochondria in these nerve cells. As an approximation, several of them are as little as one-half the diameter of the mitochondria in many tissue cells. Another point worthy of note is the close packing and large number of mitochondrial folds. While this is by no means diagnostic for

nerve cells, it is unlike the situation in the mitochondria thus far described in most other tissues. The density of intramitochondrial matrix material even within a single cell is variable from one mitochondrion to the next. The mitochondria are also considerably shorter than those found in axons (Hess and Lansing, '53).

No difference exists between the mitochondria in different cell types. The structure of this organelle will again receive attention when discussing ageing in nerve cells.

Golgi apparatus. In preparations studied with the light microscope, the Golgi apparatus, revealed by appropriate silver and osmic acid techniques, is well developed in spinal ganglion cells. A structure, similar to that described by Sjöstrand and Hanzon ('54) and Dalton and Felix ('55) in electron micrographs as the Golgi apparatus, is found in sections of spinal ganglion cells studied with the electron microscope. This material is located easily and extensively throughout the cytoplasm of spinal ganglion cells (figs. 7, 11, and 15). It occurs near the nucleus (fig. 15) as well as near the cell membrane (figs. 7 and 11), which illustrates its extensive disposition.

Its morphology is similar to the structure called the Golgi apparatus and described in other cells by Sjöstrand and Hanzon ('54) and Dalton and Felix ('55). The material consists of membranes, granules, and vacuoles (fig. 12). The membranes are similar in size to ergastoplasmic filaments. The granules, however, are clear in the center and surrounded by a more dense border, in contrast to the punctate appearance of ergastoplasmic granules. The vacuoles are the outstanding component of this structure. They are encased by the membranes and are apparently clear in the center. The size of the vacuoles appears to differ in various cells. However, this difference has not been correlated with the "dark" or "light" cell types or with the location of the Golgi complex near the nucleus or near the cell membrane.

Satellite cells

Nucleus. The nucleoplasm of the satellite cell usually presents a more or less homogeneous appearance with the dense chromatin material dispersed throughout the nucleus (fig. 17). At times, the chromatin material is not so evenly dispersed and is aggregated into several irregular clumps (fig. 8). The nucleoplasm is much more dense than that of the nerve cell.

The satellite cell nucleus is usually intimately related to the nerve cell. It is either separated from the nerve cell by its own intervening cytoplasm or rests on the nerve cell, giving the appearance of a demilune. Frequently, the satellite cell nucleus has a more intimate relation to the nerve cell and causes an indentation in the cytoplasm of the nerve cell (fig. 5).

Cytoplasm. The cytoplasm of the satellite cell is very difficult to fix. It frequently tears away from the nerve cell. At times, it appears relatively devoid of formed elements. However, favorable preparations reveal that the cytoplasm is fairly dense, containing scattered ergastoplasmic filaments and granules and mitochondria that compare in size with those of the nerve cell (fig. 8).

The satellite cell cytoplasm completely surrounds the nerve cell, even though at times it appears thin and attenuated (figs. 11 and 15).

Cell membrane. The limiting membrane of the satellite cell presents the structure typical of other cells (figs. 8, 11, and 15). The cell membrane of these cells can be divided into two parts — that apposed to the ganglion nerve cell and the surface distal to the nerve cell. Both surfaces are usually relatively smooth, the former following the contour of the ganglion cell and the latter, the surface of satellite cells belonging to neighboring nerve cells or the outlines of an intervening connective tissue capsule (figs. 11 and 15).

However, a frequent occurrence, usually near the nucleus of the satellite cell, is the appearance of a collection of membranes (figs. 13 and 17). These membranes, each of about

the same thickness as the limiting membrane of the satellite cell elsewhere, twist and fold, establishing a complex labyrinthine apparatus. There are at least two relationships of satellite cells that could account for this appearance. One is that the varied membrane appearance is due to extensive overlapping of processes of satellite cells belonging to one nerve cell and serving to form its capsule. The other view is that the complex apparatus represents local meanderings of the membranes themselves of one satellite cell. Although not definitely established, we at present tend to favor the latter viewpoint. Evidence for this is that it is possible in some sections to trace some of the membranous folds back to the surface membrane of the satellite cell. It can then be seen that both surfaces of the satellite cell membrane, that apposed to the nerve cell and that distal from it, contribute to the complex membranous apparatus. Another point in favor of this view is that the complex membranous apparatus occurs frequently near the nucleus of a satellite cell. Since the nucleus of the satellite cell is located centrally in the light microscope with approximately equal amounts of cytoplasm extending from it, the location of the complex membranous apparatus near the nucleus would indicate that it is formed locally by the membranes of one cell. Of course, it is not impossible that the overlap of cytoplasm of the satellite cells belonging to a single neuron is so extensive that processes of satellite cells can extend for long distances and reach as far as the centrally-located nucleus of an adjacent satellite cell belonging to the same neuron, yielding the folded membrane appearance.

The various relationships and appearances of the satellite cell do not appear to be restricted to a single nerve cell type, but can usually be found in relation to "dark" or "light" cells.

There are similarities between satellite cells, Schwann cells, and neuroglia. The similarities in the relationships of perineuronal glial satellites and nerve cells of the central nervous system (see Penfield, '32) and the satellite cells and spinal

ganglion nerve cells described here are striking. The nucleus and the cytoplasmic contents of the satellite cells are similar to those of Schwann cells (Hess and Lansing, '53). The indentation of the cytoplasm of the spinal ganglion cell caused by the satellite cell nucleus is reminiscent of the indenting of the axon and myelin sheath by the Schwann cell nucleus (Hess and Lansing, '53). Since the neurilemma includes the membrane of the Schwann cell (Hess, '55) and is a continuous sheath throughout the extent of the peripheral nerve fiber, the Schwann cell of adjacent internodal segments can be considered as forming a syncytium across the node of Ranvier, even though the Schwann cell cytoplasm might appear arrested at the node. Satellite cell cytoplasm surrounds the spinal ganglion nerve cell. Among histologists, the prevailing view is that the satellite cells are continuous with the neurilemma at the region of exit of the nerve process and that the satellite and Schwann cells have a common origin from the neural crest (see Singer, '54). Thus the spinal ganglion cell and its process that enters the peripheral nerve (its dendrite) are enclosed in a continuous sheath of cells. Rio-Hortega also believed in the similarities of neuroglia, satellite cells, and Schwann cells and called the latter two "peripheral neuroglia" (see Penfield, '32).

Senile spinal ganglion nerve cells

Degeneration of cells, of course, may be found in senile ganglia and these will manifest hyperchromatic nuclei, chromatolysis, etc. (see Andrew, '52). In cells that are not in the process of degeneration, the cell membrane, nuclear membrane, nucleoli, and Nissl substance do not exhibit obvious age changes. The accumulation of pigment, however, is a characteristic of all senile spinal ganglion nerve cells. In addition, it is also necessary to comment on the structure of the mitochondria since these organelles have been described as undergoing profound alterations in structure with age (Payne, '52; Weiss and Lansing, '53).

Mitochondria. Characteristic mitochondria, as found in nerve tissue (Hess and Lansing, '53), are found in spinal ganglion nerve cells with and without obvious age changes. Thus, apparently intact mitochondria are found in ganglion cells containing dense accumulations of pigment (fig. 4). The mitochondria, exhibiting normal folds, are scattered at random throughout the cytoplasm. However, we have also observed swollen and vacuolated mitochondria in senile spinal ganglion cells (fig. 3). These mitochondria conform closely to the description of Weiss and Lansing ('53) in their paper on the age changes of the anterior pituitary of the mouse. The mitochondria are several times enlarged and rounded; the matrix material is essentially lacking or very dilute as evidenced by lack of density within the mitochondria. The folds are barely recognizable as very short inward extensions from the limiting membrane or surface of the mitochondria. It is interesting to note that both the apparently intact mitochondria and the degenerative mitochondria are found in cells that appear well-fixed. This gives rise to the implication that at least some ganglion cells exhibit mitochondrial ageing (Payne, '52; Weiss and Lansing, '53). However, we have found comparable degenerative mitochondria in sections of very young (three-day-old) and adult spinal ganglion cells of guinea pigs in which pigment was absent and no age changes had occurred (fig. 13). Since degenerative mitochondria can be found in young and adult cells and normal mitochondria are seen in senile cells, it is difficult, at least for individual spinal ganglion cells, to use the condition of the mitochondria as an index of ageing.

Pigment. In the extremely senile guinea pigs we have studied, virtually all of the ganglion cells, despite cell type, contain pigment bodies in varying amounts (figs. 4 and 6). The pigment usually tends to form aggregations toward the periphery and more frequently occurs around the entire border of the cell, rather than in its interior.

The pigment bodies are characterized by very marked electron density and vary in shape from spheroidal to highly

irregular bodies. Their density approximates that of lipoidal inclusions or nucleolar material. Although the most frequent appearance is that of a homogeneous mass, there are not uncommon exceptions. The pigment bodies are usually dense and solid (figs. 4 and 10). However, in some instances, the pigment body seems to be composed of a number of vesicles of very low electron density surrounded by a lacework of dense material (fig. 6). In still other instances, the combination of the aforementioned forms occurs with the pigment body being composed of both solid and vesiculated forms (fig. 6). Vesicles can vary from one to many in a pigment body.

Beginning pigment formation seems to occur in most intimate relation with swollen mitochondria (figs. 2 and 10). This relation of mitochondria and pigment is seen not only in senile cells (fig. 2), but also in adult animals (fig. 10) where only infrequent cells exhibit small amounts of pigment. The mitochondria swell, their borders become very dense, and the internal folds disappear with the interior of the mitochondria assuming a homogeneous, less dense appearance. The pigment granules accumulate in relation to the mitochondria and extend from one pole of the mitochondria. Payne ('52) has observed that one of the first changes in ageing mitochondria is that "they appear as brown pigment-like bodies." The accumulation of pigment apparently progresses by the formation of a successive series of vesicles which then coalesce to form a pigment body. A suggested series of stages in the formation of a pigment body is presented in figures 2, 6 and 4.

SUMMARY

Ultrathin sections were made of the spinal ganglia of three-day-old, adult, and 6-year-old guinea pigs and examined with the electron microscope. Two nerve cell types are observed, mainly based on the distribution of the Nissl substance. The nucleoplasm and three components of the nucleolus of the neurons are described. The cell membrane of the nerve cell can be smooth or can present thin villiform projections

containing nerve cytoplasm. No evidence of neurofibrils is seen. Nissl substance is composed of layers of fine tubular filaments with granules apposed to them and lined up between them, similar to the appearance of ergastoplasm in other cells. The tubular elements of a Nissl body are oriented in one direction. The mitochondria are usually small, thin, and elongated and present numerous, closely-spaced folds. The main folds might present villous extensions. A structure similar to the Golgi apparatus of other cells occurs extensively throughout the cell and can be found near the nucleus and near the limiting cell membrane. It consists of membranes, granules, and vacuoles and is similar to that described in other cells.

The nucleus of the satellite cell is described. It can cause an indentation in the nerve cell cytoplasm. The satellite cell cytoplasm contains mitochondria and scattered ergastoplasmic filaments and granules. It encapsulates the neurons. The membrane of the satellite cell is described. A complex membranous apparatus, produced either by invagination and folding of the membrane of a single satellite cell or by overlapping of the processes of adjacent satellite cells, has been found, usually located near the satellite cell nucleus. A discussion is presented concerning the significance of and comparing morphological similarities of satellite cells, Schwann cells, and neuroglia.

Degenerative mitochondria can be found in young and adult nerve cells and normal mitochondria are seen in senile cells. It is difficult to use the condition of the mitochondria as an index of ageing. All senile ganglion nerve cells present pigment. The appearance and distribution of the pigment bodies are described. A suggested series of stages of pigment formation, arising from swollen mitochondria, is presented.

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PLATES

PLATE 1

EXPLANATION OF FIGURES

All illustrations are electron micrographs of the spinal ganglia of guinea pigs. All magnifications are approximate. The photographs of this plate are from ganglia fixed in Palade's ('52a) fluid.

- 1 Spinal ganglion nerve cells illustrating the nerve cell types with varying densities of cytoplasm. $\times 1000$.
- 2 Apparently swollen mitochondrion (M) in intimate relation with the supposed beginning of pigment (P) formation. $\times 12000$.
- 3 A neuron of a senile guinea pig showing swollen degenerative mitochondria (M) and pigment (P). $\times 12,000$.
- 4 A neuron of a senile guinea pig illustrating solid and dense pigment bodies (P) and intact mitochondria (M). $\times 12,000$.
5. A nerve cell and satellite cell nucleus showing the latter causing an indentation in the neuron cytoplasm. $\times 3000$.
- 6 Neuron cytoplasm of a senile guinea pig showing vesiculated bodies (P) believed to be various stages in the formation of the pigment. $\times 12000$.

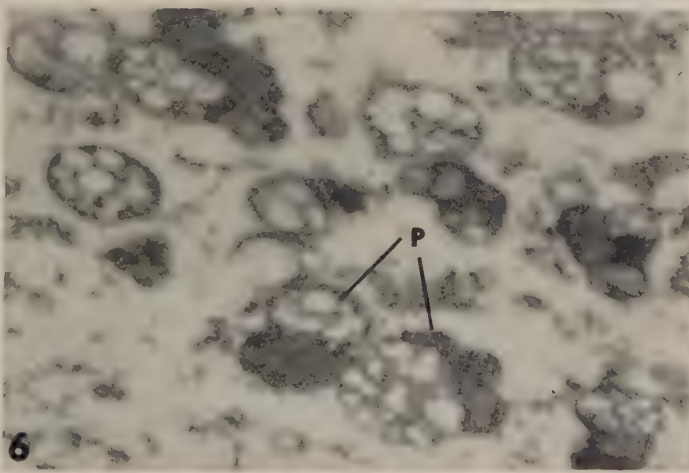
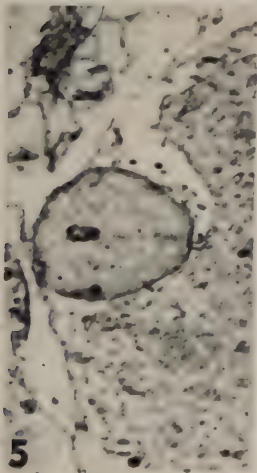
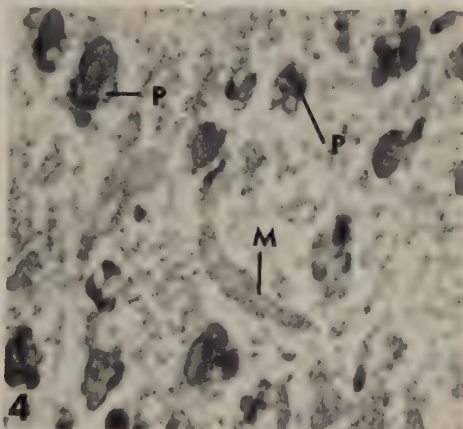
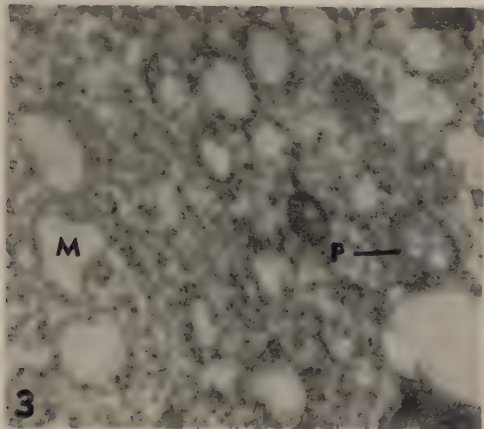
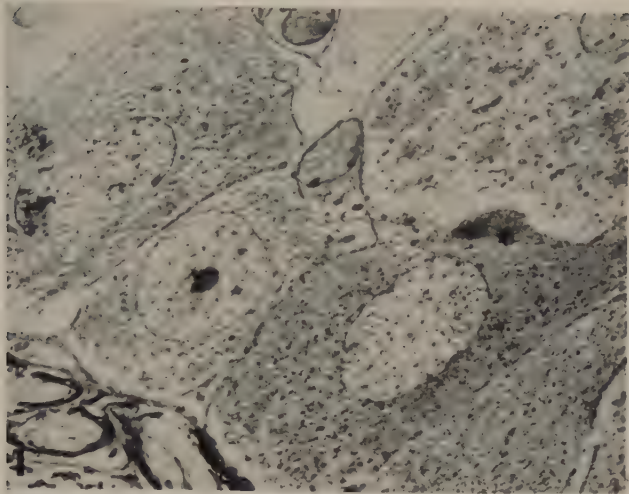


PLATE 2

EXPLANATION OF FIGURES

All illustrations are electron micrographs of the spinal ganglia of guinea pigs. All magnifications are approximate. The photographs of this plate are from ganglia fixed in Dalton's (Dalton and Felix, '55) fluid.

- 7 A "light" ganglion cell with clumped Nissl substance and villiform processes extending from the cell membrane. The Golgi apparatus (G) is seen near the cell membrane. A mitochondrion (M) is also shown. $\times 15000$.
- 8 A satellite cell nucleus with clumped chromatin. The satellite cell cytoplasm contains mitochondria and scattered ergastoplasmic filaments and granules. The satellite cell limiting membrane can also be seen. $\times 15000$.
- 9 Part of the nucleolus near the nuclear membrane of the nerve cell yielding the appearance of a nucleolar satellite. $\times 15000$.
- 10 An adult nerve cell showing beginning pigment (P) formation extending from the pole of swollen mitochondria (M). $\times 15000$.

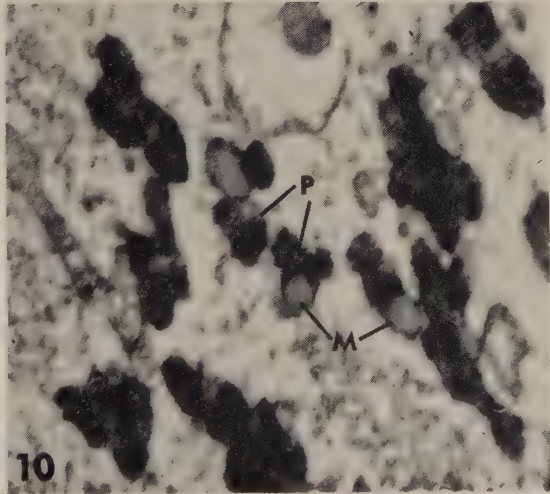
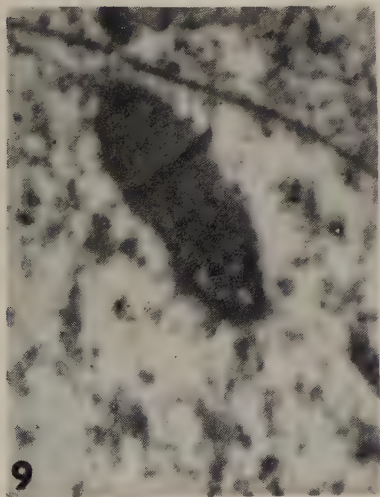
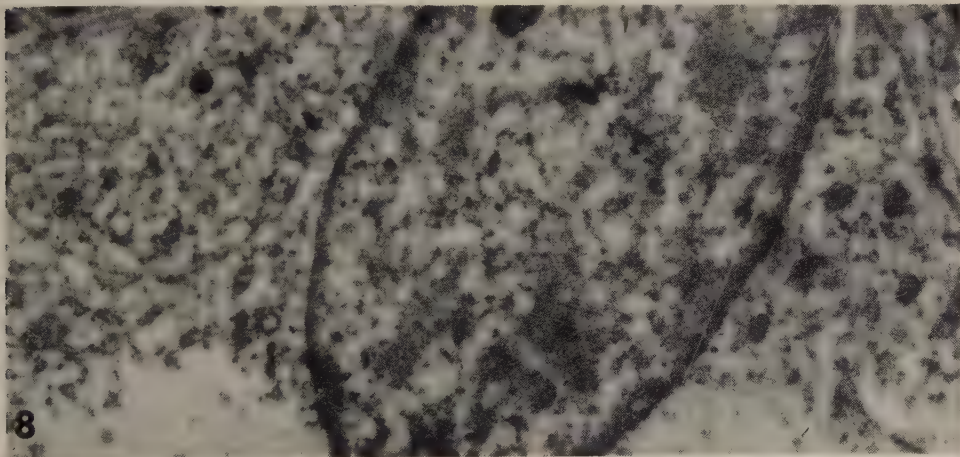
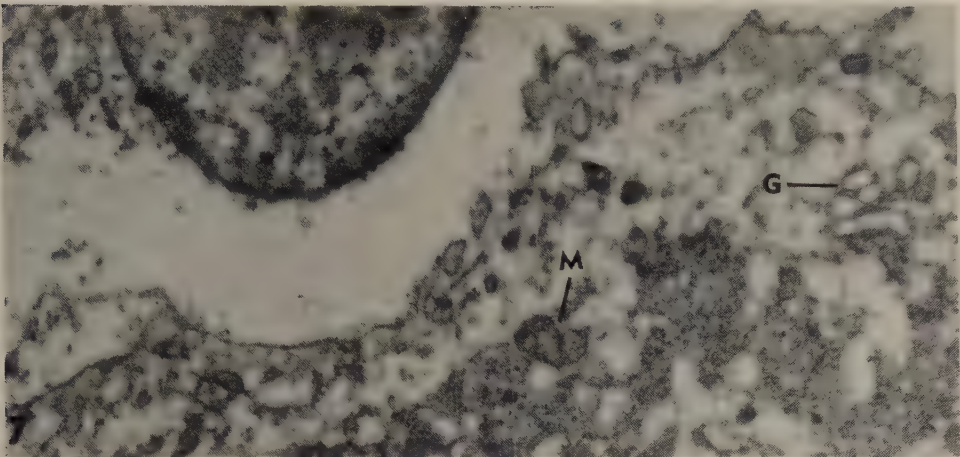


PLATE 3

EXPLANATION OF FIGURES

All illustrations are electron micrographs of the spinal ganglia of guinea pigs. All magnifications are approximate. The photographs of this plate are from ganglia fixed in Dalton's (Dalton and Felix, '55) fluid.

- 11 An illustration of the cytoplasmic contents of the "dark" cell type showing the similarity of the Nissl substance to ergastoplasm (E), ergastoplasmic filaments and punctate granules apposed to and lined in a row between the filaments, the Golgi apparatus (G) near the limiting membrane and mitochondria (M). The thin satellite cell cytoplasm (SC) encapsulates the neuron. The satellite cell limiting membrane is also shown. $\times 24000$.
- 12 An enlargement of figure 11 showing the Golgi apparatus with Golgi vacuoles (Gv), membranes (Gm), and granules (Gg). The villous folds of a mitochondrion (M) are also shown. $\times 42000$.

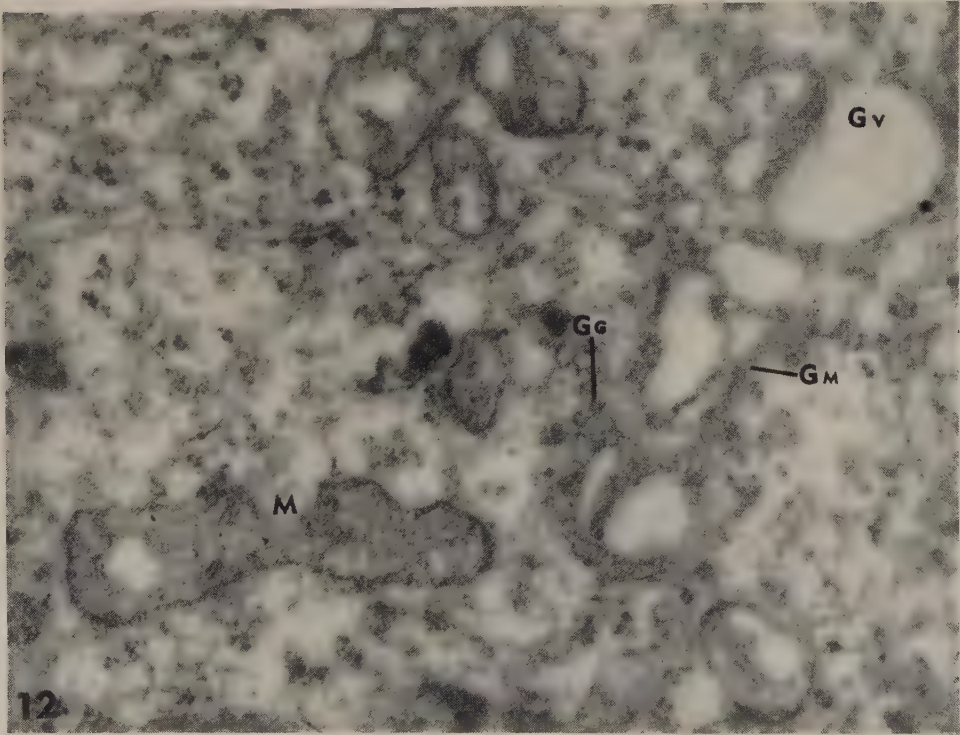
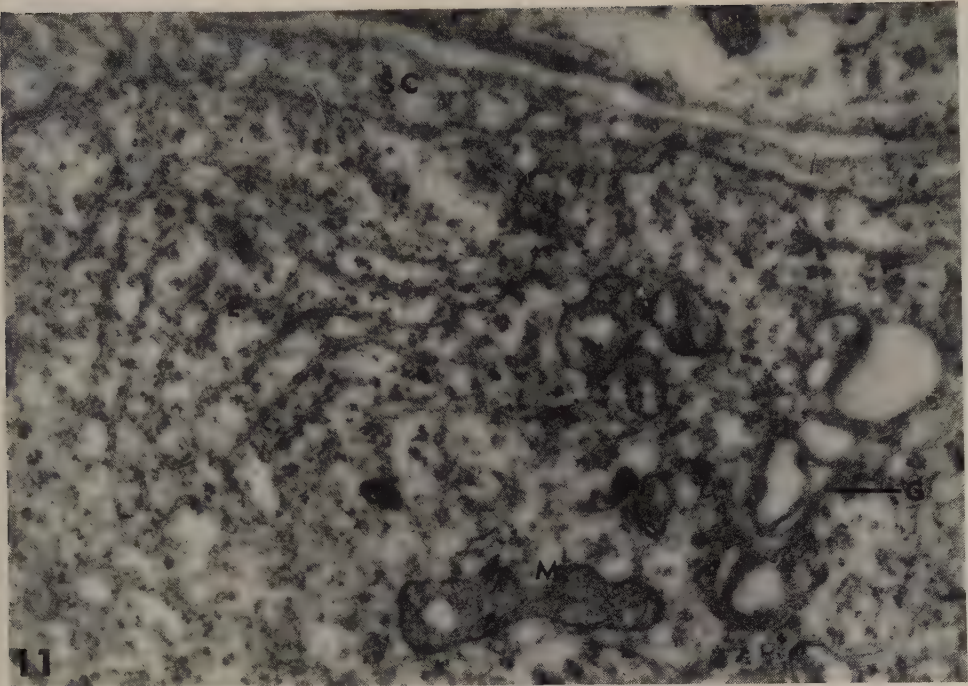


PLATE 4

EXPLANATION OF FIGURES

All illustrations are electron micrographs of the spinal ganglia of guinea pigs. All magnifications are approximate. The photographs of this plate are from ganglia fixed in Dalton's (Dalton and Felix, '55) fluid.

- 13 The complex membranous apparatus (MA) of the satellite cell cytoplasm is shown. The adult nerve cell has some swollen degenerative mitochondria (M). $\times 15000$.
- 14 A Nissl body of a "light" cell is shown and is similar to ergastoplasm with layers of filaments and granules between them. $\times 20000$.

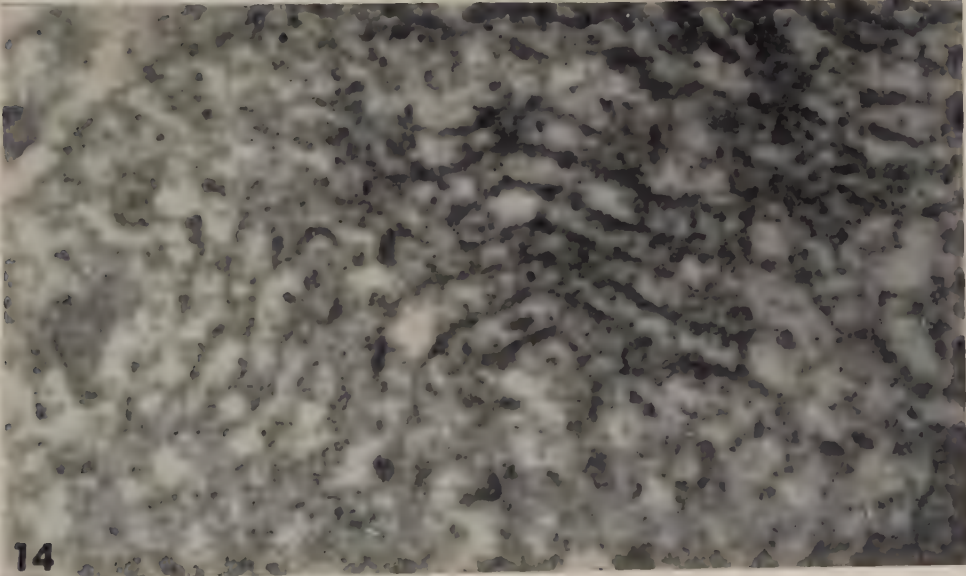
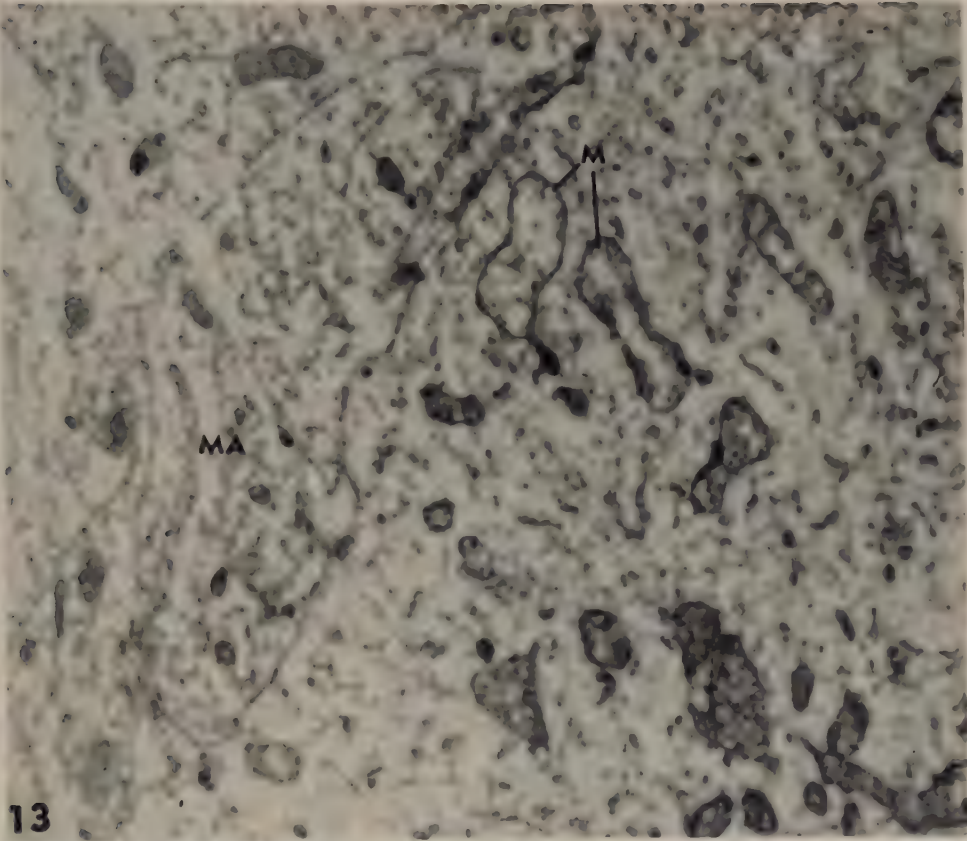
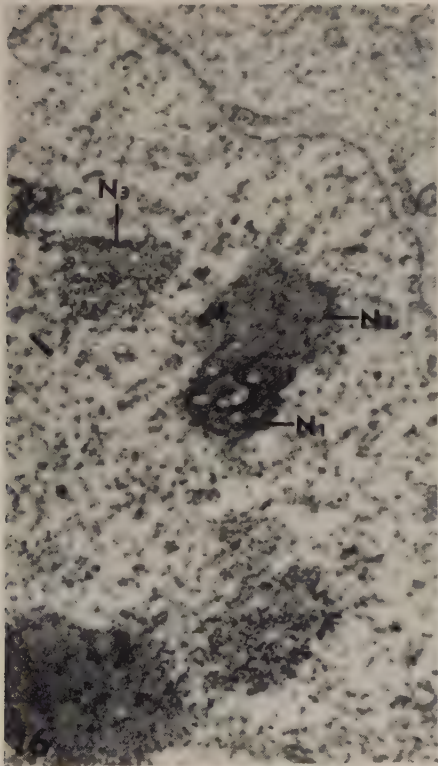
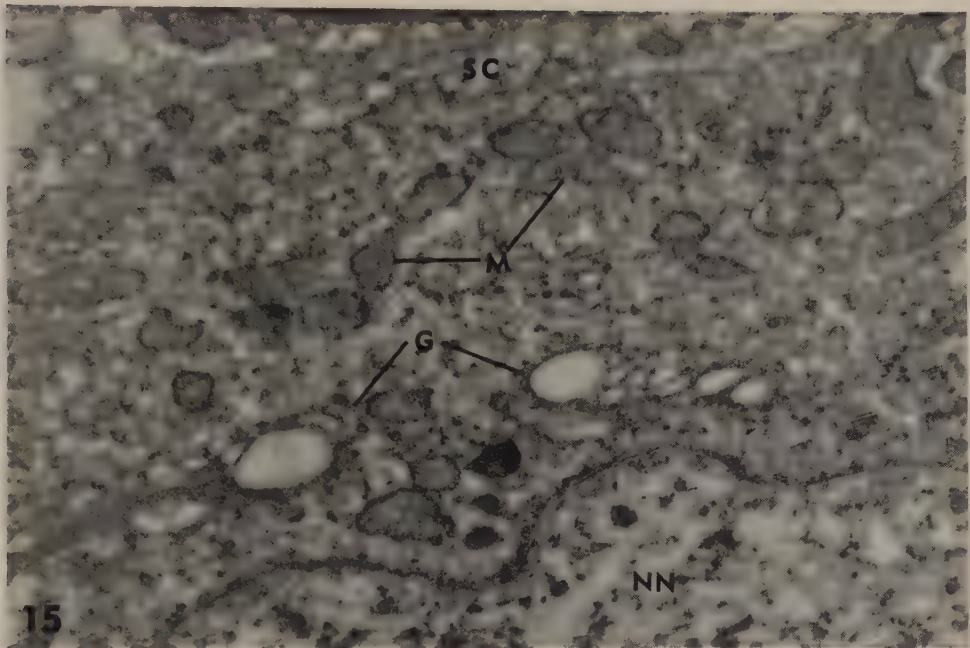


PLATE 5

EXPLANATION OF FIGURES

All illustrations are electron micrographs of the spinal ganglia of guinea pigs. All magnifications are approximate. The photographs of this plate are from ganglia fixed in Dalton's (Dalton and Felix, '55) fluid.

- 15 Cytoplasm of a "dark" cell showing the diffuse and scattered Nissl substance, Golgi apparatus (G) near the nerve cell nucleus (MN), and mitochondria (M). The double-walled structure of the nerve cell nuclear membrane is shown. The satellite cell cytoplasm (SC) encapsulates the neuron. The satellite cell limiting membrane can also be seen. $\times 20000$.
- 16 A nerve cell nucleus showing the vesicular part of the nucleolus (N_1), the irregular homogenous mass commonly associated with it (N_2), and the other irregular punctate masses (N_3). The membrane of the nerve cell nucleus is also shown. $\times 12000$.
- 17 The complex membranous apparatus (MA) of the satellite cell cytoplasm is shown near the satellite cell nucleus (SN). The satellite cell nucleus is more or less homogeneous in appearance. $\times 15000$.



THE SINO-ATRIAL NODE OF THE RAT HEART¹

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FOUR FIGURES

The vertebrate heart has been the object of considerable morphologic and functional investigation. Anatomically the structure of the heart has been carefully studied with special emphasis on the muscular modifications and their relationship to beat conduction. With each animal form studied, there has been agreement and disagreement about these specialized muscle structures and their functions. It is generally accepted that the sino-atrial node, the specialized muscle mass described by Keith and Flack ('07) lying at the junction of the right atrium and superior vena cava (right precaval vein), is present in most animals. Though many investigators confirm its presence (mouse: Nomura, '52; sheep, monkeys and man: Copenhaver and Truex, '52; various vertebrates: Davies and Francis, '46; dog and monkey: Nonidez, '43), some deny it (rat: Prakash, '54; ungulates, dog and man: Glomset and Glomset, '40; man: Todd, '32). Where the sino-atrial node has been described, it has been found intimately associated with a very definite nodal artery. During the course of study of the cardiac veins in the rat heart, the author noticed an artery from the right internal mammary artery supplying the area of the right atriocaval junction where it was assumed the sinus node should lie. Since a search of the literature failed to furnish any specific information on the sino-atrial node of the rat, this investigation was undertaken.

¹ This investigation was supported in part by research grant H-1575 from the National Heart Institute, National Institutes of Health, the United States Public Health Service.

In the meantime, a report by Prakash ('54) appeared denying the presence of a sinus node in the rat heart.

MATERIAL AND METHODS

The hearts were removed from 27 adult rats and fixed in Lavdowsky's mixture. Complete sections of the entire hearts were cut in the frontal plane at 10μ and stained with azophloxine in four-dye combination (Halpern, '54a). In addition, 55 adult rats were injected with colored latex and the vessels to the heart were dissected under low-power magnification. Sections of one rat heart were reconstructed by the wax-plate method to show the disposition of the sino-atrial node around the right atriocaval junction and the relationships of its arteries.

OBSERVATIONS

The use of azophloxine in four-dye combination facilitates the identification of nodal tissue and other specialized muscle tissue in the heart (conduction tissue). With this technic, cardiac muscle stains deep brick red whereas nodal (conduction) tissue stains pale pink to pale lavender. At the junction of the right superior vena cava with the right atrium, a lightly staining mass of tissue is seen. Tracing this mass of tissue reveals that it forms a horseshoe-shaped collar around the right atriocaval junction. It is absent dorsally, best developed on the medial (aortic) and ventral sides of the atriocaval junction, and is weakly developed laterally. Running through this mass of tissue is a conspicuous nodal artery (N.A. in fig. 1). Figure 2 is a photograph of the lateral (A) and medial (B) aspects of a wax-plate reconstruction (made at $100\times$) of this region. In A one can observe the nodal arteries applied against the surface of the right superior vena cava. These vessels are branches from either the right internal mammary artery or the right subclavian artery. The nodal artery, on the lateral aspect, penetrates the substance of the sino-atrial node and passes through it. In

B (fig. 2) the medial (aortic) aspect of the superior vena cava is shown where it enters the right atrium. The sinus node is larger and better developed on this aspect than it is laterally. The vessels labelled *nodal arteries* (fig. 2, B) are actually branches from the nodal artery to the atrial wall and anastomose with other atrial arteries that arise as a common

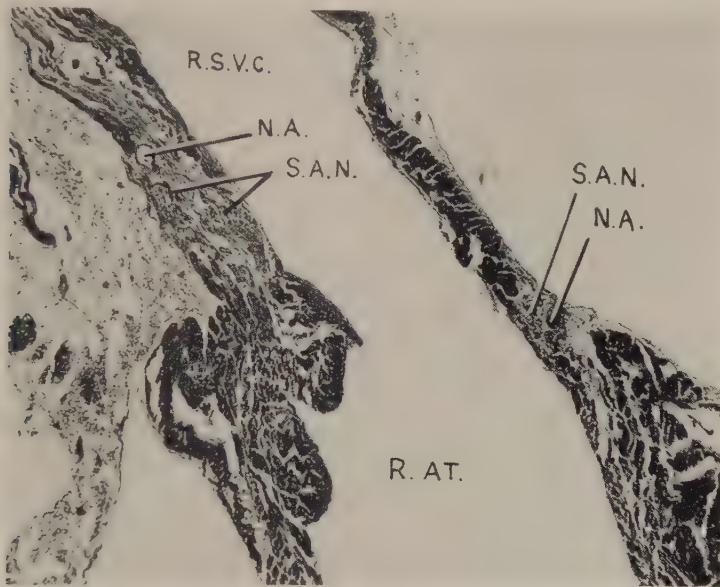


Fig. 1 Low-power view ($33\times$) of a frontal section through the rat heart at the right atriocaval junction. The medial side is at the left of the figure. The sino-atrial node (S.A.N.) is on the medial and lateral sides of the atriocaval junction. The nodal artery (N.A.) is closely related to the node. R.S.V.C., right superior vena cava; R. At., right atrium.

stem of the right internal mammary artery. This configuration is found in all the hearts studied. Since this pattern and staining distinction of the tissue was so constant, supplemental, careful high-magnification studies were made.

Morphologically, the lighter staining area consists of muscle fibers distinctly different from those which stain darkly (cardiac muscle). The light fibers are markedly smaller and contain fewer myofibrillae than cardiac muscle (fig. 3). The

photomicrograph in figure 3 shows the atrial cardiac muscle fibers (C.M.) surrounding the nodal fibers (N.F.). The nodal artery (N.A.) lies within this mass of nodal fibers (figs. 1 and 3). The node occupies the thickness of the atrial wall, extending from a subepicardial position to the subendocardium. On the lateral side, the node seems to be confined to the

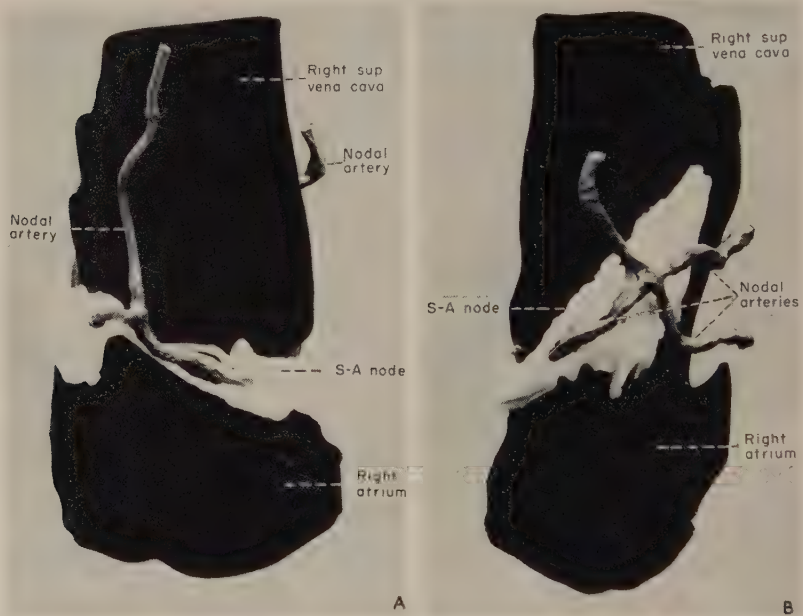


Fig. 2 Wax-plate reconstruction of the right atriocaval junction of the rat heart. A is a latero-ventral view; B is a medio-ventral view of the right atriocaval junction. The black area of the model represents the lumen of the right superior vena cava and of the right atrium. The walls of these structures are not visualized in the reconstruction.

subepicardium. At this lateral site, the nodal fibers are scattered and intermingled with the connective tissue of the nodal artery. As the node is traced from lateral, to ventral, to medial (aortic) side of the right atriocaval junction, the fibers become more numerous, spread out away from the nodal artery and fill in the entire atrial wall. In some sections the fibers appear to lie against the endocardium.

Though nodal fibers are much smaller than atrial cardiac muscle fibers, they show definite distinguishing characteristics. The myofibrillae are sparse, irregularly placed, and concentrated near the periphery of the fiber leaving a clear central area. Small granules can be seen in this clear space. The nuclei of the nodal fibers (N.F. in fig. 4, B) are round

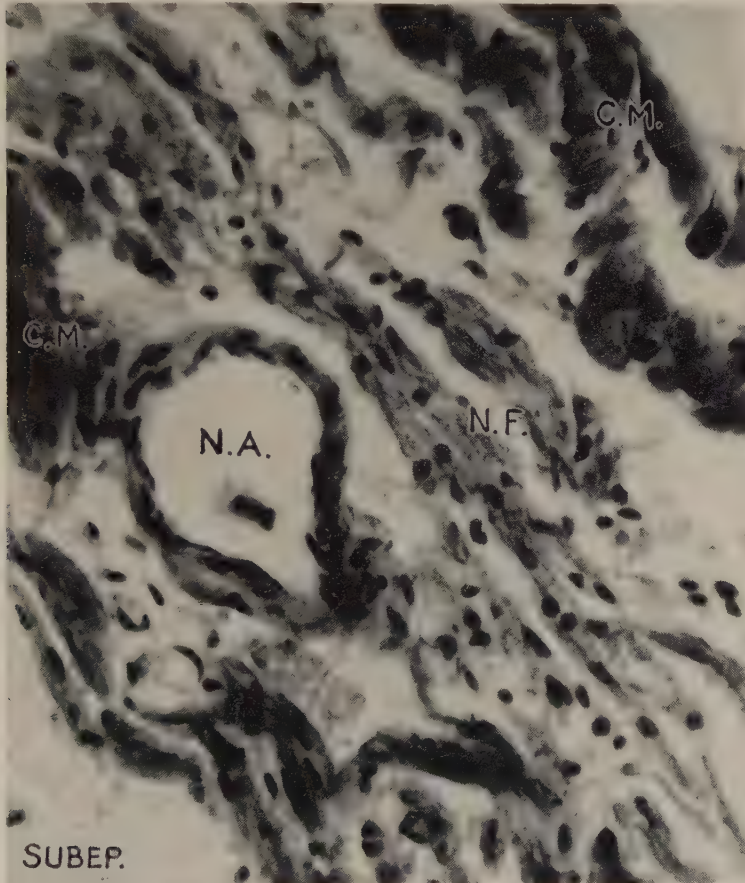


Fig. 3 Photomicrographs (400 $\times$) of the sino-atrial node and nodal artery (N.A.) from the medial side of the right atriocaval junction. The differences in size and staining reaction between nodal fibers (N.F.) and cardiac muscle fibers (C.M.) are evident. Note the relationship of the prominent nodal artery (N.A.) to the fibers of the node.

or oval, filling the entire diameter of the cell, whereas the atrial cardiac muscle (C.M. in fig. 4, B) nuclei tend to be more elongate and slender. In transverse section, the nucleus of the nodal fibers (N.F. in fig. 4, A) is ringed by a few peripheral myofibrillae. Some of the nodal fibers appear to be multinucleated. The nodal fibers do not form compact bundles as does the cardiac muscle, but tend to be more wavy and loosely arranged (figs. 1, 3, 4).

Individual nodal fibers have been traced serially and are seen to become transitional (TR. in fig. 4) and be continuous with atrial cardiac muscle fibers. The myofibrillae become more numerous and regularly placed in the transitional fibers. There is sharp contrast between the smaller nodal fibers and the larger cardiac muscle fibers which have a greater nucleocytoplasmic ratio. The transitional fibers (TR.) are of various sizes between cardiac muscle and nodal fibers. They exhibit an increasing number of myofibrillae and intensity of stain as they become continuous with the atrial cardiac muscle.

The nodal artery is interesting in that it illustrates a different concept of the blood supply to the heart. Instead of being a branch from the right coronary artery as it is in other mammals (Halpern, '54b), the nodal artery comes from an extracardiac origin. The nodal artery of the sino-atrial node in the rat heart is a branch of the right internal mammary artery (or the right subelavian artery). This branch from the right internal mammary artery follows along the right superior vena cava giving off separate vessels to the atrial musculature. It continues as a discreet nodal artery to the sino-atrial node and to the region of the right atrio-caval junction. This vessel, as determined by using differently colored latex injections masses, has no grossly visible anastomoses with the coronary arteries. The course, distribution and collateral circulation of these extracardiac coronary arteries to the rat heart and their relationships are under investigation and will be reported at a later date.

DISCUSSION

The description of the sino-atrial node as being present at the region of entry of the right precaval vein into the right atrium by Keith and Flack ('07) for several mammals, including the rat, has been shown to be valid innumerable times during the years. In the many animals studied the tissue found in this region differs considerably from the surrounding cardiac muscle and the node is easily identifiable as a distinct entity. Nomura ('52) describing the nodal systems in the mouse heart found that fibers of the sinus node all possessed a morphological similarity by having a large, clear perinuclear area, few myofibrillae and indistinct cross striations. The nodal fibers appeared paler than ordinary myocardial fibers. The fibers surrounded the nodal artery which is a branch from the right subclavian artery. Similar descriptions of the fibers of the sino-atrial node in hearts from sheep, monkeys, and man were given by Copenhaver and Truex ('52). Rather than to repeat all the previous work on this subject which verifies the presence of a sinus node in some particular animal, the reader is referred to the list of references given by Nomura ('52). Evidence for the presence of the node based on physiological as well as on anatomical investigations in various vertebrates is reviewed by Davies and Francis ('46). The greatest disagreement over the presence of the sino-atrial node is found in the studies on the cold-blooded vertebrates and on birds. In mammals, however, there is general agreement that the sinus node is present. Nevertheless there are a few dissenting reports. The most recent is by Prakash ('54) who failed to find a sino-atrial node in the rat. Instead, he claimed to have found an extensive distribution of Purkinje fibers in the atria and at the interatrial septum of the rat heart. Todd ('32) also was convinced that there were no nodes in the human heart, but instead there were atrial masses of Purkinje fibers and that no part of the right atrium was devoid of them.

In the present study, all parts of both atria were carefully examined. Expanded, light staining atrial muscle fibers are

seen scattered abundantly at random throughout the atria of the rat heart. Unless these fibers are traced individually in serial sections, one can be easily misled into thinking that they are Purkinje fibers as identified by Prakash ('54) and Todd ('32). When traced serially, these fibers are merely enlargements or expansions of portions of ordinary atrial cardiac muscle fibers, usually in the region of the nucleus. Since the nuclei of the atrial muscle fibers are surrounded by a perinuclear space where the myofibrillae diverge to pass around the nucleus, sections through these areas can be easily misinterpreted. Copenhaver and Truex ('52) found similar fibers in the atria and realized that these are only local variations in size of the atrial muscle fibers. The sinus nodal fibers bear no resemblance to these fibers and the node is distinguishable as a distinct entity on the basis of its characteristic morphology. In no other part of the atria (eliminating the atrioventricular node) of the rat heart are fibers seen that resemble the sino-atrial nodal fibers, though Glomset and Glomset ('40) stated that in the hearts of ungulates, dog, and man they found fibers typical of the nodal region in all parts of the atria.

The sino-atrial node as seen in the rat is in accord with and substantiates the observations first made by Keith and Flack ('07) and, with few exceptions, of subsequent investigators. In addition to the distinctive small, pale fibers characteristic of the sinus node, there is present a special arterial supply to these fibers. An abundance of nerves and autonomic ganglion cells are seen lying at the junction of the right superior vena cava (precaval vein) with the right atrium, in close proximity and relation to the node.

As long as differences are observed in the muscle fibers comprising the atria and other parts of the heart, whether they be conduction fibers or cardiac muscle fibers, there will be disagreement in the interpretation of these anatomic features. When the function and structure can be conclusively welded together, there will then begin to be a better understanding of what these observations on the heart represent.

Phylogenetic, embryonic, and experimental studies on the rat heart are in progress by the author. It is hoped that the results of these investigations will eventually be able to help correlate function with the morphological differences that have been observed.

SUMMARY

1. The sino-atrial node of the rat heart is a horseshoe-shaped collar lying around the right atriocaval junction.

2. The node is composed of small, wavy, pale fibers that contain few myofibrillae. The sparse myofibrillae are peripherally placed. These nodal fibers become transitional fibers which are continuous with the atrial cardiac muscle.

3. The blood supply to the sinus node is by a separate nodal artery which arises as a branch from the right internal mammary artery.

4. The large, pale fibers that are seen scattered throughout the atria are *not* Purkinje fibers as reported by Prakash ('54). When individual fibers are traced serially, they are seen to be local expansions of the atrial muscle fibers.

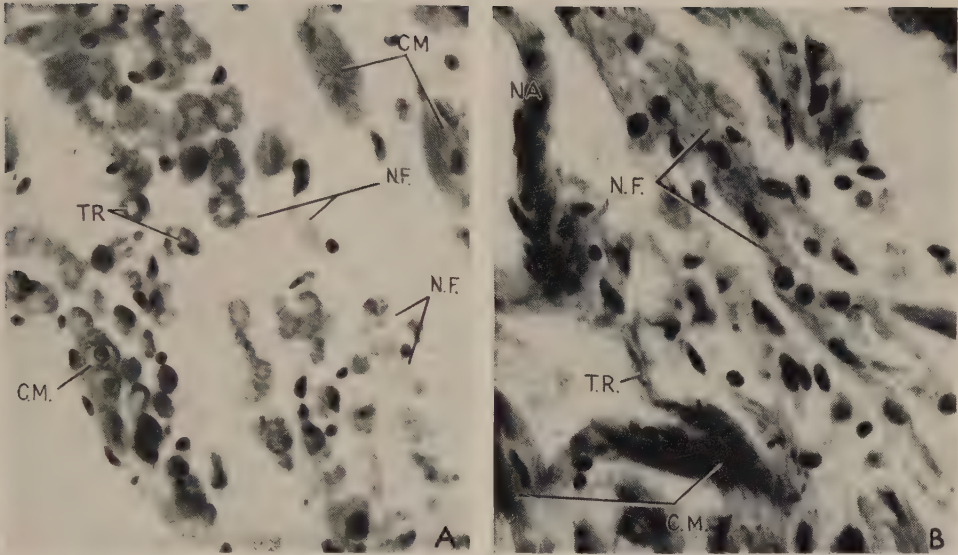
ACKNOWLEDGMENT

The author wishes to express his gratitude to Miss Joanne R. Friedlin for her excellent technical assistance during the course of this investigation.

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4 A. Transversely sectioned fibers of the sinus node (435 $\times$). The differences in size, staining reaction, and placement of myofibrillae are shown in nodal fibers (N.F.) as contrasted to cardiac muscle (C.M.) and transitional fibers (T.R.).

B. Photomicrograph (453 $\times$) of the nodal fibers (N.F.) around the nodal artery (N.A.) taken from the same field as figure 3. Transitional fibers (T.R.) intermediate between nodal fibers and cardiac muscle are shown becoming continuous with atrial cardiac muscle.

ISOLATION OF THE CARDIOINHIBITORY BRANCHES OF THE RIGHT VAGUS NERVE IN THE DOG¹

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THREE FIGURES

INTRODUCTION

Many studies (Cohn, '12; Fogelson, '28; Kisch, '44; Middleton, '50) have been devoted to the vagus nerves and their inhibitory effect on the heart. Most of them involved severing and stimulating the cervical vagi to determine their specific effect on heart action. Although the vagal afferent pathways (Whitteridge, '46, '53) and the intrinsic innervation of the heart (Wollard, '26) have received much attention, few workers have studied the specific vagal efferent pathways, especially those entering the right atrium. Barry ('35) obtained cardiac inhibition from stimulation of the right thoracic vagus but there was no mention of complete heart block. He classified the cardioinhibitory branches of the dog's vagus nerve into an upper and a lower group. The upper group arises from the vagosympathetic (caudocervical) ganglion or "above" while the lower group arises above the root of the lung and below the recurrent laryngeal nerve. Since this work concerned the existence of cardiac fibers in the pulmonary branches, no dissection or stimulation was carried out to verify the two groups of inhibitory branches. Brodie and Russell (1900) stimulated peripherally the cardiac branches of the vagi and stated that "sometimes this excitation failed

¹ These studies were aided by a contract, NR113-197, with the Office of Naval Research Dept. of the Navy.

to produce any inhibition though dissection proved that the branch in question entered the heart." Since these cardiac branches are quite small and are covered by the precaval vein (fig. 1), they are easily stretched when handling and may lead to some difficulty in producing cardiac inhibition. To overcome this difficulty the vagal trunk was sectioned at various levels and records obtained from stimulation of the segment in question. By this method the present study was undertaken to isolate the cardioinhibitory branches of the right vagus nerve.

MATERIALS AND METHODS

For the EKG recordings 10 dogs under nembutal anesthesia were employed. After a tracheotomy was performed the right pleural space was entered by resecting the 2nd, 3rd, and 4th ribs. An artificial respirator was used during each experiment. In order to isolate the thoracic vagus, the mediastinal pleura was incised and carefully lifted with a blunt forceps. Quite often it was necessary to ligate an inconstant intercostal vein that entered the precaval vein. In lifting and cleaning the nerve a glass probe was used to prevent undue damage. The various segments of the vagus nerve were stimulated with single square waves of 0.5 msec. duration. The stimuli were delivered through an isolating transformer. The records were taken with an EKG ink-writing apparatus. Leads were taken from neck to tail and from arm to arm. After each experiment the right side was dissected out and the areas of sectioning verified. Osmic acid preparations were then made of the caudovagal and craniovagal cardiac nerves, the thoracic vagus, and a few pulmonary branches. At least three experiments were discarded because of anoxia, deep anesthesia, or damage to the nerves.

RESULTS

The EKG. The left cervical vagus was first sectioned in order to prevent any cross reflexes from affecting the results. The right vagus was then sectioned in the neck and the re-

sults recorded from stimulation of its peripheral segment. The right vagus was next sectioned at or just below the origin of the recurrent laryngeal nerve and just above the origin of its pulmonary fibers. These segments, one and two (fig. 1), were stimulated and the results recorded. It was noted that segment two required about the same threshold stimulus for

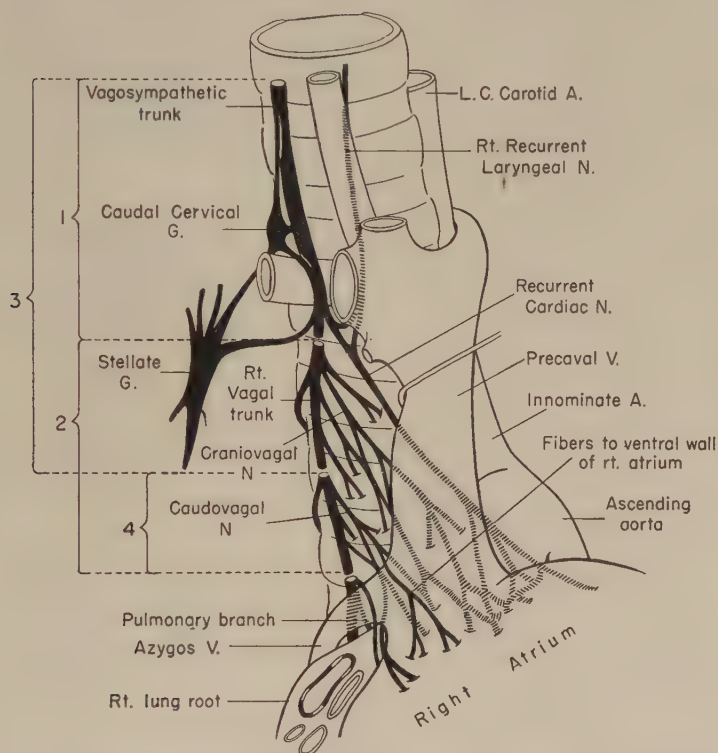


Fig. 1 Right lateral view of the thoracic vagus, showing its branches and the nerve segments stimulated.

inhibition as that of the cervical vagus (fig. 2). The voltage required to effect complete heart block was also similar in segment two and the cervical vagus (fig. 2). It was also apparent that the P wave was greatly depressed in both the threshold records (fig. 2). Segment one was then stimulated with increasing voltages with little or no effect on the beat

of the heart (fig. 2). These records were taken from the same animal and were repeated in 4 others. Although the voltages varied in each experiment, due to the depth of the anesthesia, the comparative results were similar. In 5 other animals the right vagus was sectioned at the neck and between the origins of the craniovagal and caudovagal cardiac nerves. The resulting segments 3 and 4 (fig. 1) were stimulated separately

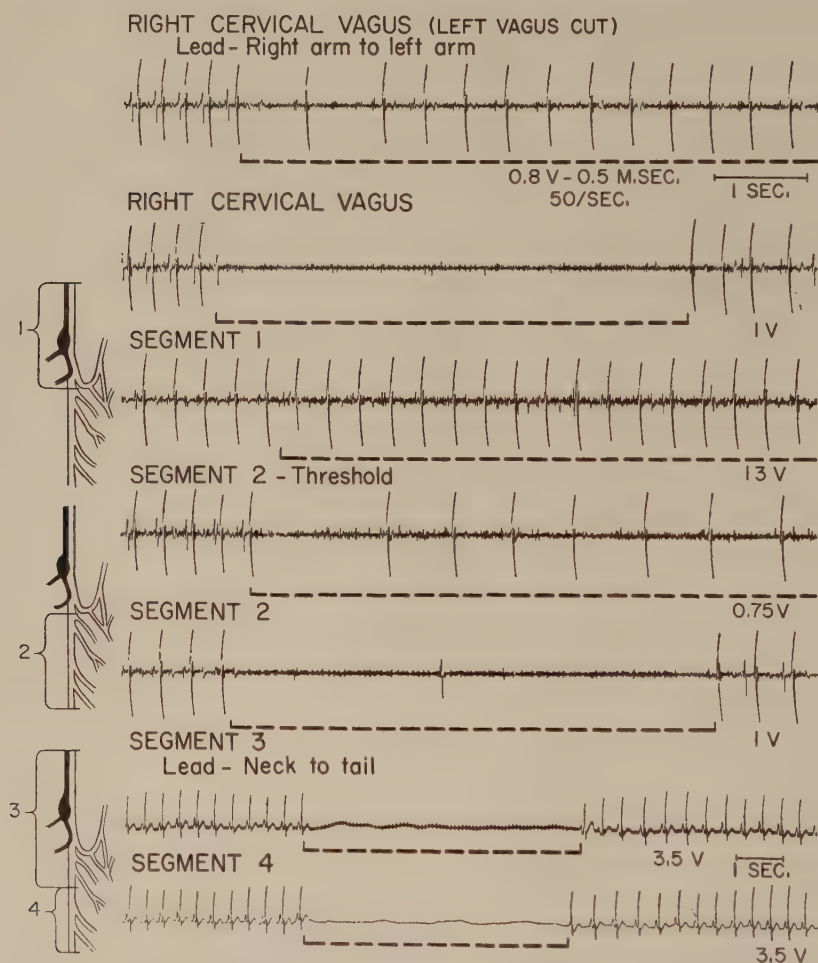


Fig. 2 EKG recordings from stimulation of the various segments of the right vagus.

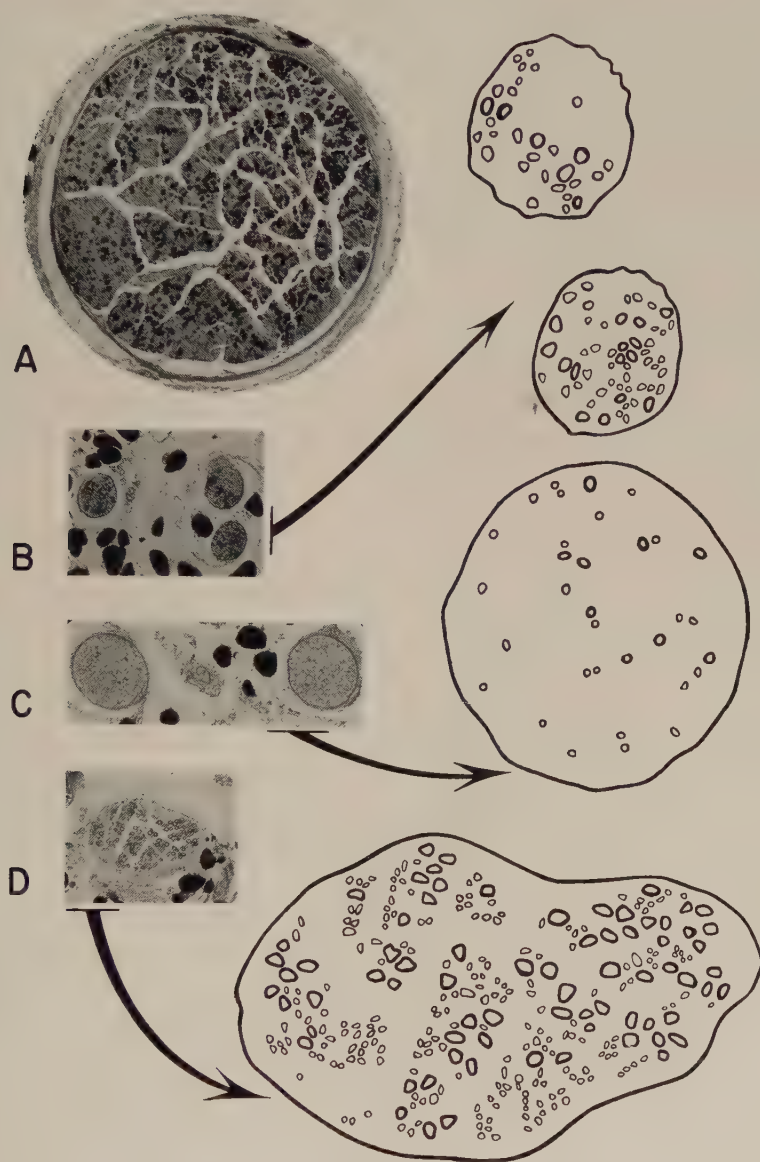


Fig. 3 Cross section of the thoracic vagus and its branches. The photomicrographs are $75\times$. Osmic acid stain.

A. Thoracic vagus.

B. Caudovagal cardiac nerves.

C. Craniovagagal cardiac nerves.

D. Pulmonary branch.

with relatively low voltages. Either segment effected a complete heart block (fig. 2).

The craniovagal and caudovagal cardiac nerves. Osmic acid preparations of these nerves (fig. 3, B and C) show a paucity of myelinated fibers, especially when compared with a pulmonary branch (fig. 3, D). The relative sizes of the caudovagal and craniovagal nerves can be ascertained by comparison with the thoracic vagus (fig. 3, A). Measurements of the myelinated fibers agree with those of Heinbecker and O'Leary ('33). Most of the myelinated fibers fell within the range of 2-5 μ . Only a few were 10 μ or more. It was also noted that the number of myelinated fibers was variable and inconstant in the craniovagal and caudovagal cardiac nerves.

DISCUSSION

Previous personal studies ('55) have shown that the cervical vagus and sympathetic trunk lie in the same epineurial sheath. Although the two trunks are separate fascicles only in the lower cervical region, Chase and Ranson ('14) state that the two trunks remain independent throughout, with connections rather than communications between the two trunks. Taking advantage of this concept, by incising the epineurial sheath, vagal and sympathetic components can be followed under binocular dissection to determine whether the cardiac nerve in question is composed of one or the other or both kinds of fibers. It was observed that the thoracic vagus gave rise to two groups of nerves entering the dorsal and ventral walls of the right atrium. These nerves were named the craniovagal and caudovagal cardiac nerves (fig. 1). Schurawlew ('29) and Nonidez ('39) in their excellent work illustrated only the craniovagal group and Jarisch and Zotterman ('48) in a diagram possibly indicated the caudovagal group. Chase and Ranson ('14) and Langley ('03) agree that few, if any, sympathetic fibers course in the thoracic vagus and that the greater number of non-medullated fibers is due to a loss of the myelin sheath and the emergence of

most of these medullated fibers via the recurrent laryngeal nerve. Heinbecker and O'Leary ('33) in the cat and Evans and Murray ('54) in the rabbit present similar evidence. It may be assumed from this evidence and the fact that there are few myelinated fibers in these cardiac nerves that the majority of the fibers are vagal preganglionics.

Threshold stimulation of the peripheral segment of the right cervical vagus results in inhibition of the heart and a strong depression of the P wave (fig. 2). Stimulation of segment two (fig. 2) gave identical results in the same animal. The depression of the P wave represents an inhibition of the atrial impulse indicating a thoracic emergence of the atrial inhibitory impulses. Both the right cervical vagus and the thoracic vagus were stimulated with the same voltage resulting in complete arrest of the heart, providing further evidence that the branches of the thoracic vagus carry the inhibitory fibers to the right atrial wall.

Upon stimulation of segment one (fig. 2) no inhibition, even with high voltages, was evidenced in 4 of the 5 dogs. In the one animal there was some inhibition of the heart indicating that inhibitory fibers may course in the recurrent cardiac nerve (fig. 1). This idea was supported by the fact that after severing the origin of the recurrent laryngeal nerve (fig. 1) stimulation no longer elicited any inhibitory effect. The anatomical basis for this effect was later verified by dissection. In the 5 other animals stimulation of segments 3 and 4 (fig. 2) indicate that the craniovagal and caudo-vagal cardiac nerves have a similar inhibitory action on the heart. From these recordings it may be suggested that these cardiac nerves innervate the SA node.

SUMMARY AND CONCLUSIONS

In 10 experimental animals the right vagus nerve was sectioned at different levels and stimulated to determine the course of emergence of the inhibitory fibers. Osmic acid preparations show that the fibers of the craniovagal and caudo-vagal cardiac nerves are largely non-myelinated fibers. The

studies of Chase and Ranson ('14) and Langley ('03) indicate that these are preganglionic fibers of the thoracic vagus. Evidence is presented to indicate that the majority of inhibitory fibers to the right atrium course in the craniovagal and caudovagal cardiac nerves arising below the origin of the right recurrent laryngeal nerve. Stimulation of these nerves at relatively low voltages caused a complete arrest of the heart. These nerves may possibly innervate the SA node.

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MORPHOGENETIC STUDIES OF THE RABBIT.

XIII. THE INFLUENCE OF THE DWARF GENE UPON ORGAN SIZE AND VARIABILITY IN RACE X¹

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Dwarfism in man has been recognized since the time of the Egyptian, Khoumhatpon or about 2500 B. C. according to Dupertius ('45), but most of the available information concerns body size and proportions and only more recently, some of the causative factors. Anthropomorphic measurements of 100 human dwarfs have been studied by Dupertius ('45) and a few of the clinical studies on human dwarfism are: Schaeffer ('36), Greene ('51), Milne ('51), and others. Data on organ weights in human dwarfs seem to be entirely lacking.

External measurements of cattle are described by Crew ('24), Lush ('30), Mead et al. ('42) and Johnson et al. ('50); and for sheep, Bogart and Dyer ('42). Variations in size and body proportions in various breeds of dogs including measurements of the endocrine glands and skeleton, were studied by Stockard ('41). In the domestic fowl, there is the excellent work of Landauer ('38, '39a and '39b) and the more recent work of Pun ('54). These studies on the chicken give data on weights of internal organs, but due to the lethal action of the dwarf gene, these data include only the late fetal and newly-hatched chicks.

¹ This investigation was supported (in part) by research grants from the American Cancer Society on the recommendations of the Committee on Growth of the National Research Council, and the National Cancer Institute of the National Institutes of Health, Public Health Service.

The first report on dwarfism in any rodent is that of Sollas ('09) on dwarfism in the guinea pig and this has been followed by the studies of Snell ('29), Smith and MacDowell ('30 and '31), Boettiger and Osborn ('38), Helweg-Larsen and Nielsen ('50) and others working with the dwarf mouse. Dwarfism in the rat has been reported by Lambert and Sciuchetti ('35) and Woolley ('48). At least 5 dwarf types in the rabbit have been described by Sawin ('55), all of which appear to be transmitted by single mutated genes, each inducing a slightly different syndrome of manifestations, but none of these have been studied with reference to their effects upon adult organ size. An earlier report on dwarfism in the rabbit by Schnecke ('41) and the report by Sawin review much of the earlier literature on genetic studies of dwarfism in the rabbit. The Dw gene to be discussed here was first described by Greene et al. ('34) as a Mendelian lethal recessive but subsequent studies by Greene ('40), Crary and Sawin ('49) and Latimer and Sawin ('55a) have shown that the heterozygotes can be distinguished from the homozygotes, thus indicating incomplete or partial dominance.

A few organ weights of homozygous, heterozygous and normal siblings were studied by Greene ('40) and by Pearce and Brown ('45) but due to the death of the homozygous dwarf individuals at, or shortly after birth the study was restricted to this age. Crary and Sawin ('49) noted that although this gene did not affect the order of appearance of the ossification centers of the long bones of this race of rabbits (race X) in the heterozygous state as compared with homozygous normals, it did affect the time of ossification and length and diameter of digital bone development. Until now the effects of the single dose of the dwarf gene on the weights of the internal organs have never been followed in later development.

Included in the group of 100 adult rabbits of race X (Latimer and Sawin, '55b), there were 15 males and 20 females carrying a single dose of the dwarf gene (Dw), and this explains to a degree the variability observed in this

race. A differential influence of this gene upon the central nervous system has been reported by Latimer and Sawin ('55a) and this present study is a further analysis of the differential influences of the heterozygous state of this gene upon the other parts and organs.

MATERIALS AND METHODS

The 100 rabbits of race X used in this study have been described together with the details of the dissections (Latimer and Sawin, '55b) and these need not be repeated here. Each of the 100 rabbits was studied consecutively, irrespective of its normal or dwarf condition, thus insuring less bias in making the measurements. The gross body weight is the weight of the live rabbit just before anesthetization and the net body weight is the gross body weight minus the weight of the contents of the digestive tube and all fat which could be removed by gross dissection. The living dwarf rabbits are easily recognized by their shorter ear length (Crary and Sawin, '49).

Weights and linear measurements

The external proportions of the body of the fetal and newborn homozygous dwarfs (DwDw) described by Greene ('40) and Pearce and Brown ('45) suggest achondroplastic dwarfism, but in neither paper are any measurements given. To see if these adult heterozygous dwarfs (Dwdw) of race X, which will be designated as "dwarfs" throughout this paper, showed any evidence of the short and wide head and shortened extremities observed at birth by Greene, these measurements were studied from a series of external measurements which will be reported later. None of these measurements in either sex were significantly different when compared with normals of the same sex. The cephalic indices were slightly, but not significantly greater in the dwarfs, which means that the transverse diameter of the head in the dwarfs is very slightly greater, relative to the head length, than it is in the normal rabbits, and slightly greater in the dwarf

males than in the dwarf females. The lengths of each extremity in terms of body length were not significantly different in the dwarfs. In both sexes, the fore limbs and hind limbs of the dwarfs were slightly, but not significantly longer, relative to body length, than in the normal rabbits. All but one of the "t" values of these differences were below 0.5, hence we may conclude that the external proportions of these adult dwarfs resemble the proportions of the normal adults.

The body weights, organ weights and linear dimensions of the 35 normal males and 30 normal females are shown in table 1, and in table 2 similar data for the 15 male and 20 female dwarf rabbits. In both tables, the averages with their standard deviations and coefficients of variation are shown for the males and females with the "t" values of the differences between the sexes. The sex with the greater dimension is indicated with the "t" values and the levels of significance of the "t" values are stated at the bottom of each table.

A comparison of the data in tables 1 and 2 shows that the normal males average 17% greater in body weight and 6% longer than the dwarf males. The similar differences for the females are 29% and 11% respectively, or the females are affected much more by this dwarf gene than the males. With this disparity in body size, one would expect to find the organs larger in the normals and such is the case with two exceptions, namely male hypophysis and eyeballs which are heavier in the dwarf males than in the normal males. All of the organs are larger in the normal females. These relationships will be considered further in table 5.

The data in table 1 show that the gross body weight of the normal females averages 25.8% greater than the same measurement in normal males. The net body weight in the normal females is 18.7% greater, and the normal female body length is 7.1% greater. Due to this sex difference, one would expect to find the organs heavier in the females and this is the case with the exception of two organs; the gonads and harderian

glands. All but 5 of the organs in table 1 are significantly heavier in the females.

The similar measurements for the male and female dwarf rabbits in table 2 show much less sex difference. The gross body weight of the dwarf females is but 8% greater than that of the males or but about one-third of the difference found in the normal rabbits, and not statistically significant. The net body weight is but 2.2% greater in the dwarf females or about one-ninth of the difference in the normal rabbits. There is likewise not as much difference in the nose-anus length, for the dwarf females are but 2.3% greater than the males, compared to a difference of 7.1% in the normal rabbits. In these dwarf rabbits there are 15 measurements greater in each sex but only three of these, trunk, pancreas and fat are significantly greater in the females. The gonads and harderian glands are the only two organs which are significantly heavier in the males and these are the only two organs which are heavier in the normal males (table 1).

The individual organs of the normal and dwarf rabbits differ in their degree of variability and often the variability of the same organ will differ markedly in the two sexes. However these coefficients of variation in table 1 for the normal rabbits average exactly the same in the two sexes or 18.33%. In table 2, the average of the coefficients of variation for the males is 18.95% and for the dwarf females, 17.00%. There is, however, a large range in the coefficients of variation of the individual organs in the dwarf rabbits, or from 4.5% for the male body length to 58.9% for the ovaries.

The data in tables 1 and 2 seem to indicate that the dwarf gene reduces the body size and organ size in the females more than in the males and that organ weights are slightly less variable in the dwarf females. The relations of the absolute weights of the organs in normal and dwarf rabbits of the same sex will be further discussed in connection with table 5.

TABLE 1

Weights in grams and lengths in millimeters of the parts and organs of 35 male and 30 female normal rabbits

	MALES		FEMALES			"t" ¹
	Average, gm or mm and stand. dev.	Coef. var.	Average, gm or mm and stand. dev.	Coef. var.		
Body weight gross	1972 ± 274	13.91	2480 ± 345	13.93	♀	6.64
Body weight net	1650 ± 215	13.01	1959 ± 231	11.78	♀	5.55
Body length	464 ± 21	4.49	497 ± 16	3.27	♀	7.06
Head weight	117 ± 13	10.85	126 ± 7.1	5.59	♀	1.04
Trunk weight	1152 ± 161	13.97	1502 ± 246	16.39	♀	6.93
Fore limbs weight	73.6 ± 11.8	16.07	86.4 ± 8.6	9.94	♀	1.54
Hind limbs weight	287 ± 39	13.74	351 ± 37	10.56	♀	6.66
Integument	247 ± 49	19.64	264 ± 33	12.62	♀	4.13
Musculature	927 ± 137	14.74	1163 ± 150	12.86	♀	6.65
Skeleton, lig.	180 ± 24	13.32	207 ± 14	6.89	♀	0.54
Skeleton, cart.	117 ± 15	12.42	132 ± 8	6.14	♀	1.55
Fat	118 ± 58	48.90	278 ± 153	55.03	♀	5.72
Dig. tube weight	86.44 ± 11.09	12.83	99.17 ± 11.24	11.83	♀	4.55
Dig. tube contents	208.1 ± 33.4	16.07	239.9 ± 61.9	25.81	♀	2.62
Dig. tube length	4114 ± 384	9.32	4434 ± 295	6.66	♀	3.69
Liver	70.542 ± 15.989	22.67	79.408 ± 21.822	27.48	♀	1.88
Pancreas	4.547 ± 1.315	28.92	5.827 ± 1.687	28.95	♀	3.41
Heart	4.485 ± 0.708	15.78	5.125 ± 0.720	14.05	♀	3.58
Spleen	0.526 ± 0.208	39.55	0.679 ± 0.212	31.25	♀	2.91
Thyroid	0.133 ± 0.030	22.37	0.167 ± 0.045	27.21	♀	3.54
Suprarenals	0.299 ± 0.102	34.14	0.366 ± 0.108	29.61	♀	2.53
Hypophysis	0.0267 ± 0.0055	20.49	0.0415 ± 0.0121	29.21	♀	6.48
Gonads	3.836 ± 1.413	36.85	0.505 ± 0.283	56.02	♂	12.50
Uterus		..	9.665 ± 3.412	35.30	..	..
Kidneys	15.472 ± 2.996	19.36	17.905 ± 3.206	17.90	♀	3.14
Bladder	1.202 ± 0.253	21.07	1.572 ± 0.351	22.35	♀	4.89
Eyeballs	5.002 ± 0.416	8.32	5.734 ± 0.600	10.47	♀	5.75
Harderian glands	1.704 ± 0.486	28.51	1.639 ± 0.199	12.17	♂	0.68
Brain	9.265 ± 0.459	4.95	9.755 ± 0.493	5.05	♀	4.12
Spinal cord, weight	3.945 ± 0.365	9.26	4.537 ± 0.377	8.31	♀	6.37
Spinal cord, length	281 ± 12	4.32	289 ± 10	3.21	♀	6.46

¹"t" values of 2.00 and above are significant at 5% and values of 2.66 and above are significant at 1%.

TABLE 2

Weights in grams and lengths in millimeters of the parts and organs of 15 male and 20 female dwarf rabbits

	MALES		FEMALES		"t" ¹
	Average, gm or mm and stand. dev.	Coef. var.	Average, gm or mm and stand. dev.	Coef. var.	
Body weight, gross	1631 ± 234	14.36	1762 ± 220	12.46	♀ 1.71
Body weight, net	1368 ± 196	14.36	1398 ± 139	9.98	♀ 0.53
Body length	434 ± 19	4.47	444 ± 20	4.59	♀ 1.57
Head weight	98.8 ± 12.9	13.00	95.4 ± 6.8	7.15	♂ 1.01
Trunk weight	954 ± 141	14.75	1057 ± 113	10.69	♀ 2.40
Fore limbs weight	59.4 ± 8.0	13.44	57.6 ± 7.7	13.44	♂ 0.67
Hind limbs weight	232 ± 37	15.99	241 ± 26	10.75	♀ 0.85
Integument	218 ± 39	17.99	195 ± 33	17.11	♂ 1.90
Musculature	754 ± 130	17.19	801 ± 94	11.74	♀ 1.24
Skeleton, lig.	146 ± 16.5	11.30	149 ± 13.8	9.26	♀ 0.43
Skeleton, cart.	94.1 ± 11.4	12.15	94.2 ± 8.3	8.79	♂ 0.03
Fat	98.1 ± 46	46.36	208 ± 83	39.97	♀ 4.62
Dig. tube weight	75.45 ± 16.09	21.33	72.45 ± 8.54	11.79	♂ 0.71
Dig. tube contents	164.6 ± 47.7	28.95	160.5 ± 25.9	16.12	♂ 0.33
Dig. tube length	3620 ± 404	11.21	3600 ± 216	6.00	♂ 0.20
Liver	61.626 ± 18.726	30.39	57.972 ± 15.854	27.35	♂ 0.82
Pancreas	3.599 ± 0.889	24.70	4.414 ± 0.974	22.07	♀ 2.54
Heart	3.927 ± 0.588	14.22	3.770 ± 0.293	7.76	♂ 1.08
Spleen	0.407 ± 0.137	33.62	0.385 ± 0.119	30.83	♂ 0.49
Thyroid	0.0897 ± 0.0232	25.91	0.1014 ± 0.0313	30.87	♀ 1.22
Suprarenals	0.288 ± 0.097	33.72	0.276 ± 0.092	33.15	♂ 0.36
Hypophysis	0.0275 ± 0.0078	28.40	0.0281 ± 0.0077	27.56	♀ 0.002
Gonads	3.224 ± 1.055	32.71	0.298 ± 0.176	58.88	♂ 12.24
Uterus	...	...	5.606 ± 1.697	30.27	...
Kidneys	13.559 ± 2.049	15.11	13.058 ± 1.429	10.94	♂ 0.84
Bladder	1.008 ± 0.214	21.19	1.022 ± 0.178	17.43	♀ 0.21
Eyeballs	5.102 ± 0.512	10.04	5.116 ± 0.283	5.53	♀ 0.10
Harderian glands	1.151 ± 0.214	18.58	0.951 ± 0.291	30.61	♂ 2.24
Brain	8.849 ± 0.610	6.90	8.740 ± 0.577	6.50	♂ 0.54
Spinal cord weight	3.915 ± 0.438	11.19	3.926 ± 0.359	9.15	♀ 0.08
Spinal cord length	267 ± 13	4.89	273 ± 12	4.49	♀ 1.63

¹"t" values of 2.03 and above are significant at the 5% level and values of 2.72 and above are significant at the 1% level.

The weights of the individual organs of each specimen were reduced to percentages of the net body weight and these percentages of the normal and dwarf males and females are shown in tables 3 and 4 in the same manner as in the preceding tables. The preponderance of heavier female organs is now reduced so that in table 3 there are but 10 organs heavier in the females (6 significantly heavier) and 16 greater in the males, and of these 16 organs, 6 are significantly heavier namely, head, integument, gonads, harderian glands, cartilaginous skeleton and brain. In the dwarf males (table 4) 19 organs are heavier and of these 5 are significantly greater, namely, head, integument, gonads, harderian glands and heart. Thus the head, integument, gonads and harderian glands are relatively heavier in both normal and dwarf males and these organs may be thought of as distinctly male parts, with the cartilaginous skeleton and brain heavier in the normal males and the heart significantly heavier in the dwarf males.

Similarly there are 6 organs (trunk, musculature, fat, hind limbs, hypophysis and bladder) significantly greater in the normal females. In the dwarf females, but 4 organs are significantly greater, namely, trunk, musculature, fat and pancreas. Thus the heavier trunk, musculature and fat are common to both normal and dwarf females, with the hind limbs, hypophysis and bladder reduced by the dwarf gene and the pancreas significantly enlarged.

The averages of the coefficients of variation of the percentage weights of the male and female organs in the dwarf rabbits (table 4) are practically the same as the averages of the coefficients for the normal rabbits in table 3, or 15.6% for the males and 17.5% for the females, and all of these percentage weights are less variable than the weights in grams. These relative weights will be discussed more fully in connection with table 6 which will be presented in proper sequence.

In table 5 the absolute weights of the parts and organs of the dwarf males and females (table 2) are listed as percentages of the absolute weights or lengths of the same parts in

the normal animals of the same sex (from table 1). The "t" values indicate the significance of the differences between the absolute measurements of the normal and dwarf animals of the same sex.

Every measurement in the females is smaller in the dwarf rabbits than in the normals, and these percentages range from the dwarf female spleen which is but 57% of the spleen weight in the normal female to the spinal cord length which is 91% of the length of the cord in the normal female. All of these differences between the measurements of dwarf and normal females are significant except for the fat, which is so variable that the difference is not significant. There are 5 organs in the female dwarfs which are less than two-thirds of the size of the same organ in the normal females; they are in decreasing order of percentage: thyroid, ovaries, uterus, harderian glands and spleen. All of these are organs of marked variability, with the thyroid and harderian glands the least variable.

The differences in the males are not as great. Two of the organs in the males, hypophysis and eyeballs are actually slightly larger in the dwarfs than in the normal males, and there are 7 measurements in the males which are not significantly different. The greatest difference is in the thyroid, which is significantly smaller and but 67% of the weight of the thyroid in normal males. The organs in the dwarf males average 85.8% of the similar organ weights in the normal males, and the females average 72.6%. Thus the dwarf gene reduces the organ weights an average of 27.4% in the females and but 14.2% in the males. This is further evidence of the greater effect of the dwarf gene on female rabbits.

Table 6 follows the same plan as table 5, except that the percentages of the net body weight are used rather than the weights in grams. This should show more adequately the relative differences in these dwarf animals compared to the normals of the same sex, and should more clearly reveal the effects of the dwarf gene, if it does have a differential effect, on the various parts and organs in the dwarf rabbits. The

TABLE 3

Percentages of the net body weight in 35 male and 30 female normal rabbits

	MALES		FEMALES		"t" ¹
	Average % and stand. dev.	Coef. var.	Average % and stand. dev.	Coef. var.	
Head weight	7.14 ± 0.37	5.18	6.49 ± 0.47	7.22	♂ 6.15
Trunk weight	69.80 ± 2.73	3.90	76.41 ± 5.51	7.21	♀ 6.16
Fore limbs weight	4.45 ± 0.34	7.70	4.43 ± 0.29	6.65	♂ 0.25
Hind limbs weight	17.38 ± 0.99	5.72	17.96 ± 1.17	6.51	♀ 2.13
Integument	14.89 ± 1.58	10.62	13.51 ± 1.14	8.45	♂ 3.91
Musculature	56.05 ± 2.19	3.91	59.35 ± 3.13	5.27	♀ 4.90
Skeleton, lig.	10.98 ± 1.08	9.82	10.66 ± 0.95	8.95	♂ 1.24
Skeleton, cart.	7.15 ± 0.64	8.89	6.81 ± 0.60	8.80	♂ 2.17
Fat	6.78 ± 3.23	47.63	20.67 ± 5.84	28.26	♀ 11.90
Dig. tube weight	5.27 ± 0.50	9.50	5.12 ± 0.75	14.65	♂ 0.93
Dig. tube contents	12.70 ± 1.92	15.09	12.48 ± 4.45	35.61	♂ 0.25
Liver	4.29 ± 0.88	20.42	4.02 ± 0.85	21.19	♂ 1.23
Pancreas	0.273 ± 0.061	22.40	0.298 ± 0.077	25.92	♀ 1.43
Heart	0.272 ± 0.022	8.03	0.263 ± 0.033	12.71	♂ 1.28
Spleen	0.0318 ± 0.0115	36.27	0.0351 ± 0.0113	32.25	♀ 1.14
Thyroid	0.0081 ± 0.0015	18.01	0.0086 ± 0.0023	27.25	♀ 0.97
Suprarenals	0.0179 ± 0.0048	26.78	0.0187 ± 0.0055	29.36	♀ 0.62
Hypophysis	0.0016 ± 0.0004	23.10	0.0021 ± 0.0005	25.31	♀ 4.07
Gonads	0.227 ± 0.067	29.68	0.0251 ± 0.0125	49.98	♂ 15.92
Uterus		..	0.490 ± 0.146	29.72	..
Kidneys	0.938 ± 0.133	14.19	0.918 ± 0.156	16.97	♂ 0.55
Bladder	0.073 ± 0.011	15.26	0.081 ± 0.016	19.92	♀ 2.35
Eyeballs	0.307 ± 0.031	9.96	0.295 ± 0.033	11.14	♂ 1.49
Harderian glands	0.103 ± 0.023	22.58	0.085 ± 0.013	15.60	♂ 3.70
Brain	0.571 ± 0.071	12.36	0.504 ± 0.057	11.29	♂ 4.14
Spinal cord weight	0.241 ± 0.022	9.19	0.233 ± 0.022	9.21	♂ 1.39
Spinal cord length % of B. L.	60.5 ± 1.49	2.47	60.1 ± 1.62	2.70	♂ 1.02

¹ "t" values of 2.00 and above are significant at 5% level and values of 2.66 and above are significant at 1% level.

TABLE 4

Percentages of the net body weight in 15 male and 20 female dwarf rabbits

	MALES		FEMALES		"t" ¹
	Average % and stand. dev.	Coef. var.	Average % and stand. dev.	Coef. var.	
Head weight	7.23 $\pm$ 0.33	4.60	6.84 $\pm$ 0.39	5.70	♂ 3.11
Trunk weight	69.75 $\pm$ 2.86	4.10	76.05 $\pm$ 3.16	4.15	♀ 6.08
Fore limbs weight	4.34 $\pm$ 0.15	3.36	4.13 $\pm$ 0.41	9.89	♂ 1.90
Hind limbs weight	16.93 $\pm$ 0.82	4.87	17.21 $\pm$ 1.47	8.54	♀ 0.66
Integument	15.90 $\pm$ 1.30	8.21	13.88 $\pm$ 1.41	10.14	♂ 4.61
Musculature	54.94 $\pm$ 3.01	5.48	57.24 $\pm$ 2.86	5.00	♀ 2.30
Skeleton, lig.	10.78 $\pm$ 0.90	8.35	10.65 $\pm$ 0.65	6.07	♂ 0.38
Skeleton, cart.	6.91 $\pm$ 0.50	7.17	6.76 $\pm$ 0.46	6.83	♂ 0.92
Fat	7.05 $\pm$ 2.97	42.20	14.53 $\pm$ 5.38	37.04	♀ 4.85
Dig. tube weight	5.62 $\pm$ 1.47	26.18	5.20 $\pm$ 0.62	11.96	♂ 1.15
Dig. tube contents	12.19 $\pm$ 3.70	30.39	11.52 $\pm$ 1.80	15.65	♂ 0.71
Liver	4.53 $\pm$ 1.26	27.91	4.16 $\pm$ 1.13	27.26	♂ 0.91
Pancreas	0.263 $\pm$ 0.051	19.47	0.315 $\pm$ 0.061	19.35	♀ 2.67
Heart	0.288 $\pm$ 0.024	8.48	0.270 $\pm$ 0.020	7.22	♂ 2.42
Spleen	0.0295 $\pm$ 0.0077	26.25	0.0276 $\pm$ 0.0087	31.35	♂ 0.67
Thyroid	0.0065 $\pm$ 0.0013	19.45	0.0072 $\pm$ 0.0018	25.41	♀ 1.18
Suprarenals	0.0211 $\pm$ 0.0069	32.61	0.0201 $\pm$ 0.0074	36.67	♂ 0.41
Hypophysis	0.00199 $\pm$ 0.00039	19.77	0.00201 $\pm$ 0.00053	26.19	♀ 0.12
Gonads	0.234 $\pm$ 0.070	29.71	0.022 $\pm$ 0.014	63.75	♂ 13.33
Uterus		..	0.402 $\pm$ 0.118	29.20	..
Kidneys	1.005 $\pm$ 0.196	19.55	0.939 $\pm$ 0.106	11.28	♂ 1.28
Bladder	0.074 $\pm$ 0.010	13.27	0.073 $\pm$ 0.012	16.29	♂ 0.08
Eyeballs	0.376 $\pm$ 0.036	9.68	0.368 $\pm$ 0.031	8.49	♂ 0.70
Harderian glands	0.085 $\pm$ 0.013	14.87	0.068 $\pm$ 0.020	29.40	♂ 2.74
Brain	0.654 $\pm$ 0.060	9.20	0.629 $\pm$ 0.052	8.24	♂ 1.32
Spinal cord weight	0.288 $\pm$ 0.023	8.08	0.282 $\pm$ 0.024	8.43	♂ 0.75
Spinal cord length % of B. L.	61.6 $\pm$ 1.94	3.16	61.5 $\pm$ 1.64	2.68	♂ 0.17

¹ "t" values of 2.03 and above are significant at 5% level and values of 2.72 and above are significant at 1% level.

TABLE 5

Measurements of the dwarf rabbits as percentages of the similar absolute measurements of the normal rabbits. The "t" values of the differences are shown

	MALES		FEMALES	
	Percentages of normal weights	"t" values of differences ¹	Percentages of normal weights	"t" values of differences ¹
Body weight, gross	82.7	4.20	71.0	8.24
Body weight, net	82.9	4.32	71.4	9.73
Body length	93.5	4.76	89.3	10.20
Head weight	84.7	4.67	75.4	15.81
Trunk weight	82.8	4.09	70.4	7.55
Fore limbs weight	79.7	4.19	67.4	12.73
Hind limbs weight	80.8	4.55	68.7	11.52
Integument	88.3	2.02	73.9	7.17
Musculature	81.3	4.15	68.9	9.61
Skeleton, lig.	81.1	4.97	72.0	14.42
Fat	83.0	1.18	74.8	1.87
Digestive tube weight	87.3	2.77	73.0	9.03
Digestive tube contents	79.1	3.66	66.9	5.42
Digestive tube length	87.7	4.18	81.2	10.83
Liver	87.4	1.70	73.0	4.26
Pancreas	79.2	2.51	75.8	3.38
Heart	87.6	2.68	73.6	7.97
Spleen	77.4	2.01	56.7	5.62
Thyroid	67.2	5.04	60.8	5.60
Suprarenals	96.3	0.36	75.7	3.02
Hypophysis	103.0	0.41	67.7	4.38
Gonads	84.0	1.48	59.0	2.87
Uterus	..	..	58.0	5.15
Kidneys	87.6	2.22	73.0	6.33
Bladder	83.7	2.56	65.0	6.51
Eyeballs	102.0	0.72	89.2	4.29
Harderian glands	67.5	4.17	58.0	9.93
Brain	95.5	2.63	89.6	6.66
Spinal cord weight	99.2	0.24	86.5	5.72
Spinal cord length	95.0	3.62	91.3	8.38

¹"t" values of 2.01 and above are significant at 5% and values of 2.68 and above are significant at 1%.

"t" values indicate the significance of the differences between the percentage weights of the organs of the normal (table 3) and dwarf (table 4) rabbits of the same sex.

Over half of all the percentage measurements in both sexes or, 67% in the males and 56% in the females are not significantly different in the dwarfs compared to the normals of the same sex. In the males there are only 8, or one-third of the total number of measurements significantly different, with 6 of the 8 significantly larger in the dwarfs. Of the 11

TABLE 6

Organ weights relative to net body weight in the dwarf rabbits compared to similar percentages in the normal rabbits of the same sex

	MALES		FEMALES	
	% of normal	"t" 1 values	% of normal	"t" 1 values
Head weight	101.3	0.80	105.4	2.73
Trunk weight	99.9	0.06	99.5	0.26
Fore limbs	97.5	1.18	93.2	3.02
Hind limbs	97.4	1.52	95.8	1.99
Integument	106.8	2.15	102.7	1.01
Musculature	98.0	1.45	96.4	2.39
Skeleton, lig.	98.2	0.62	99.9	0.04
Fat	104.0	0.28	70.3	3.72
Dig. tube weight	106.6	1.27	101.6	0.39
Dig. tube contents	96.0	0.63	92.3	0.90
Liver	105.6	0.77	103.5	0.50
Pancreas	96.3	0.55	105.7	0.82
Heart	105.9	2.27	102.7	0.83
Spleen	92.8	0.70	78.6	2.48
Thyroid	80.7	3.55	83.9	2.20
Suprarenals	117.9	1.87	107.5	0.76
Hypophysis	121.3	2.92	95.3	0.65
Gonads	103.1	0.33	87.6	0.81
Uterus	..	..	82.0	2.31
Kidneys	107.1	1.40	102.3	0.52
Bladder	101.2	0.27	90.7	1.76
Eyeballs	122.5	6.84	125.0	7.83
Harderian glands	82.3	2.80	80.7	3.45
Brain	114.5	3.92	124.8	7.79
Spinal cord weight	119.5	6.70	121.0	7.41

¹"t" values of 2.01 and above significant at 5% and values of 2.68 and above significant at 1%.

female measurements which are significantly different, only 4 are larger and 7 are smaller in the dwarfs.

The brain, cord and eyeballs are significantly greater in both sexes and in addition the hypophysis, heart and integument are significantly heavier in the dwarf males. The head is the only additional part significantly heavier in the female dwarfs. The relatively larger spinal cord together with the larger brain and eyeballs may indicate a differential influence on a primary germ layer. The relatively larger heart in the dwarf males could be associated with a greater general activity which has been observed in this group.

The thyroid and harderian glands are significantly smaller in both sexes and these two are the only parts of the male dwarfs which are significantly smaller, but in the females the following parts are also significantly smaller: fore limbs, musculature, fat, spleen and uterus.

Thus the dwarf gene which reduces the size of both sexes, not only appears to reduce the size of most organs and parts more in the female than in the male, but it also affects certain parts more than others. The central nervous system apparently is relatively unaffected by it, whereas the thyroid and harderian glands are markedly affected in both sexes. It is also evident that certain differences appear to be sex-specific and not a part of the general size difference. The hypophysis and gonads are relatively larger in the dwarf males and relatively smaller in the dwarf females. The thyroid is the only one of the endocrine glands which is significantly smaller in both sexes in these dwarfs. Its percentage weight of 81 is the lowest percentage in the males and it is also low (84%) in the females, but not the lowest. Whether the larger male hypophysis and gonads are in any way associated with a recognized greater sexual interest in the dwarf male as compared with the dwarf female, or whether they are a part of the general imbalance induced by the thyroid deficiency, is a matter of speculation at this time.

The most outstanding quantitative differences in both sexes are the relatively larger central nervous system and the much

smaller thyroid in the dwarf rabbits, with over half of the organs not significantly different in relative size.

DISCUSSION

The literature on human dwarfs, so far as it is known, provides little aid in the interpretation of the present data, for it is limited to the external dimensions and therapeutic treatment of dwarfism. Sayers and Brown ('54) state that primordial dwarfism, sometimes called "miniatures" or "midgets," may be genetically transmitted, or may occur sporadically and without a deficiency in the adeno-hypophyseal tropins. The external measurements of these adult heterozygous dwarf rabbits, so far as studied, show no evidence of achondroplastic dwarfism, although the external proportions of the newborn rabbits with the lethal, or double dose of the dwarf gene have been described by Greene ('40) and Pearce and Brown ('45) as achondroplastic dwarfs.

Greene ('40) and Pearce and Brown ('45) list a few organ weights in the normal and lethal dwarf newborn rabbits and in addition Greene gives weights and percentage weights of the same organs in the heterozygotes, but only for the newborn. These data on the heterozygotes show the same trends as in the lethal or homozygous dwarfs but to a lesser degree. The hypophysis forms the same proportions of the body weight in the normal and dwarf newborn rabbits according to Pearce and Brown; it is smaller in Greene's dwarfs and it is relatively larger in the male and smaller in the female adult dwarfs of race X. The thyroid is relatively smaller in two series of dwarfs and it is not reported in the third series. The brain, heart and kidneys are relatively larger in all three series. The liver, suprarenals and spleen are variable in their percentage weights in the three series.

There are a few organ weights in adult dwarfs of other animals recorded in the literature. Lush ('30) reports the thyroid and suprarenals in dwarf cattle within the normal range of weights, but the hypophysis is smaller than usual. Smith and MacDowell ('30) find the thyroid in dwarf mice

greatly reduced in relative size, also the anterior lobe of the hypophysis and the suprarenal cortex; the gonads are smaller although variable. Helweg-Larsen and Nielsen ('50) report no significant difference in the weights of the liver, kidneys and pancreas relative to body weight in dwarf mice.

The adenohipophysis is usually credited with the production of the growth hormone (Sayers and Brown, '54) and it has been shown in table 6 that there is a reduction in the relative weight of the entire hypophysis in dwarf females of race X, together with a reduction in body weight and in many of the organs. The relative weight of the hypophysis in the dwarf males is larger than in the normal rabbits, but there is still a reduction in body weight and in many of the organs, though to a lesser degree than in the females. It must be remembered, however, that these weights are for the entire hypophysis and not for the adenohipophysis.

The relatively smaller thyroid gland in both sexes might suggest cretinoid dwarfism, but the general body proportions and the earlier ossification of the skeletal elements in the dwarfs of this race reported by Crary and Sawin('49) would tend to refute this, though these thyroids of both sexes, significantly reduced in relative size, still suggest some type of dysfunction. Most of the changes in the weights of the organs relative to net body weight are rather insignificant and many could be explained by the smaller size of the entire animal. Many organs are relatively larger in animals of lesser body weight (Brown, '29, p. 630).

With the exception of a few organs such as the relatively larger central nervous system and the relatively smaller thyroid glands in these dwarf rabbits, they might be classified as miniatures or primary dwarfs. Only one-third of the organs in the males are significantly changed from the percentage weights of the normal males and but 44% are significantly different in the females. Their external dimensions appear to be proportionately reduced. Paschkis, Rakoff and Cantarow ('54) in discussing *manosoma vera* state: "Whether or not the genetic influence on size is transmitted

through any gland of internal secretion is unknown." The data available from these dwarf rabbits suggests primary dwarfism but more histological and physiological studies are needed before final conclusions can be made.

Many experimental studies (Smith and MacDowell, '31; Hughes, '44; Goddard, '48; Strong, '48; and Helweg-Larsen and Nielsen, '50) indicate that dwarfism can be alleviated, at least to a degree, by adeno-hypophyseal implants or extracts, and it would be interesting to see the effects of similar studies on these dwarf rabbits. Also, histological studies on the anterior hypophysis and thyroid glands of these dwarf rabbits would help to elucidate the present data. Without any histological or physiological information on these dwarf endocrine glands we may only conclude that in this race of rabbits, the dwarf gene in the heterozygous condition, reduces the body size more in the females than in the males, with the general bodily proportions maintained, together with approximately normal proportions of the majority of the organs. A few organs show significant changes in relative weight.

SUMMARY

Thirty-five adult rabbits of race X carrying the dwarf gene in the heterozygous condition are compared with 65 normals of the same race. The normal males average 17% greater in gross body weight and the normal females, 29% than the dwarfs of the same sex. The cephalic index and the lengths of the two extremities with reference to body length show no significant differences as compared to normal rabbits. Thus these adult dwarf rabbits evidence no external resemblance to the achondroplastic dwarfism reported by others for newborn rabbits of this race.

The dwarf gene reduces not only the body size but also the organ weights more in the females than in the males, thus decreasing the sex differences in the dwarfs compared to the normals.

The percentages of net body weight indicate that the brain, spinal cord and eyeballs are significantly greater in the dwarfs of both sexes, and in the males the integument, heart and hypophysis are significantly larger in the dwarfs as compared to the normals of the same sex. The head is also significantly greater in the female dwarfs.

The thyroid and harderian glands are significantly smaller in both sexes and in addition there are 5 other organs in the females which are significantly reduced, namely: musculature, fore limbs, uterus, fat and spleen. The dwarf gene apparently affects some organs differently in the two sexes, for the hypophysis is relatively larger in the dwarf males and relatively smaller in the females. Likewise the gonads are relatively larger in the males and smaller in the dwarf females.

The external proportions and the relative weights of the majority of the organs would seem to indicate that these heterozygous adult dwarf rabbits may be classified as miniatures or primordial dwarfs or *nanosoma vera*.

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HORMONAL INFLUENCES ON SEX DIFFERENTIATION IN THE TOAD, *BUFO AMERICANUS*¹

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TWENTY-THREE FIGURES

INTRODUCTION

The analysis of hormonal influences on sex differentiation in the toads is made difficult by late differentiation of their sex glands. At the completion of metamorphosis, when in most other amphibians the sexes can be clearly identified macroscopically, the gonads of toads usually must be sectioned, and one can distinguish between developing ovaries and testes only by careful histologic examination. Even so, an element of uncertainty often remains, because of incompleteness of morphologic differentiation. Since administration of hormones in high dosages further retards gonadal development, it is desirable to prolong the larval period. While the animals are still aquatic, hormonal treatments can be continued. There are two methods by which metamorphosis may be prevented: (1) by using anti-thyroid compounds, such as thiourea; (2) by removal of the thyroid. Thiourea was found disadvantageous because of its stimulating effect on the hypophysis and gonads, especially the testes (Delsol, '52; Hanaoka, '54). Thyroidectomy, preventing metamorphosis but not affecting the development of gonads (Allen, '18), appears to be a more satisfactory solution and was used in the present experiments.

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Earlier studies of hormonal effects centered on the development of the peculiar upper lobe of the toad gonads, the so-called Bidder's organ. Since this segment consists exclusively of ovarian cortex (Witschi, '33), it seems of interest to observe the effects that might be produced by treatments with androgens. Gallien ('47), and more recently Talluri and Padoa ('53) found that testosterone propionate at a concentration of 100 μ g/1 failed to masculinize this structure although its size was somewhat reduced in male as well as in female larvae. Unfortunately, hormonal treatments were always discontinued at metamorphosis and hence do not exclude possibilities of later effects in either the main part of the gonads or the cortical lobes. Therefore, the present investigation extends the study of sex differentiation under hormonal influences to postmetamorphic stages.

MATERIALS AND METHODS

The eggs of *Bufo americanus* used in these experiments were obtained in the laboratory by induced ovulation. Groups of 30 larvae were placed in aquaria each containing 6 l of dechlorinated water at a room temperature of 20°C. The crystalline hormones, estradiol or methyltestosterone, were dissolved in absolute ethyl alcohol and added to the aquarium water. Hormones and water were renewed every other day.

Removal of the thyroid primordia was performed on tadpoles of stages 21-22,² measuring 6-7 mm in length. The operation was successful in 355 cases; 105 thyroprivic larvae survived to the end of experiments. High mortality occurred after the age of three months. The nonoperated larvae completed metamorphosis within 35 to 40 days. At this time the thyroprivic tadpoles were significantly larger than controls.

Hormonal treatments were initiated at the time of closure of the gill sacs, just before feeding started (stage 25). The experiments were carried out with three series: (1) estradiol;

² The numeral system of Witschi ('49) for designation of developmental stages of anurans was adopted for the corresponding stages of the toad larvae.

(2) methyltestosterone; and (3) controls. The first two series were subdivided into groups according to the hormonal concentrations as follows:

A. Estradiol series

a. 100 $\mu\text{g}/1$ b. 500 $\mu\text{g}/1$ c. 1000 $\mu\text{g}/1$

B. Methyltestosterone series

a. 20 $\mu\text{g}/1$ b. 50 $\mu\text{g}/1$ c. 500 $\mu\text{g}/1$

C. Control series

Each group consists of normal and thyroprivic tadpoles. Treatments for normal tadpoles were discontinued after metamorphosis, but some animals were preserved only one to three months later in order to allow complete differentiation of the gonads. During this postmetamorphic period the little toads were kept on O-Cel-O sponge pads and fed with beef liver and fruit flies. All thyroprivic tadpoles were preserved at ages ranging from 120 to 150 days (table 1).

Most animals were preserved in Bouin's fixative and stained with Mallory's triple stain. A few were fixed in Flemming's osmic acid solution and stained with safranin and light green, for study of the adrenals.

RESULTS

A. Sex differentiation of the gonads

1. *Controls.* At the end of metamorphosis (stage 33), the sex glands of toads are not well differentiated, thread-like organs. The testis has a distinct medulla but often still retains cortical remnants (fig. 1). Migration of gonidia from the cortex toward medulla is in progress. The ovary contains a definite cortex and several ovarian sacs; the germ cells are still at the gonial stage (fig. 2).

As the animals grow to 4 months or older, the gonads in both normal and thyroprivic lots enlarged considerably and can be ascertained by examination under a dissecting microscope. Histologically no differences between the gonads of intact and thyroprivic animals is recognizable (figs. 3, 4, 5, 6).

TABLE 1

*Summary of sex distribution in controls and experimental groups of toads.
Normal and thyroidectomized lots*

HORMONES	DOSE	SEX RATIO					REMARKS
		♂	♂ ↘	♀	♂ +	♀	
Estradiol	$\mu\text{g/l}$						
	100a					59	Preserved at end of metamorphosis.
	b	2	1	6	2	10	Hormone discontinued at end of metamorphosis; animals preserved 3 months later.
	c*			2	1	16	Treated continuously for 4 months.
	500a	(55 not differentiated)					Preserved at end of metamorphosis.
	b*	2		5	1	8	Treated continuously for 4 months.
	1000a	(47 not differentiated)					Preserved at end of metamorphosis.
	b*	6	3	3		5	Treated continuously for 4 months.
Methyl-testosterone	20a	13		1		9	Preserved 3 weeks after metamorphosis.
	b*	4				4	Treated continuously for 4 months; preserved 1 month after discontinuation of hormone.
	50a	30		5		38	Preserved at end of metamorphosis.
	b*	(18 nearly sterile animals)					Treated continuously for 4 months.
	c*	1				1	Treated continuously for 120 days, and preserved 2 months after discontinuing hormone.
	500a	(88 not differentiated)					Preserved at end of metamorphosis.
Controls	a	24				28	Preserved at end of metamorphosis.
	b	16				15	Preserved 3 months after metamorphosis.
	c*	12				13	Preserved at ages ranging from 4 to 5 months.

* Thyroidectomized.

2. *Larvae treated with estradiol.* The moderate dose of 100 $\mu\text{g}/\text{l}$ shifts the sex ratio distinctly in the female direction. All 59 animals autopsied at the completion of metamorphosis were females, while controls of the same age consisted of 52 males and 56 females, a ratio close to normal sex distribution. The thyroprivic group, treated continuously for 4 months, consisted of 16 females and three larvae with abnormal gonads. Histologic examination proves that the latter are intersexes (figs. 7, 8). These three cases suggest a tendency of reverting toward testicular differentiation after metamorphosis, in spite of continued estradiol treatments.

Although estradiol at this dosage feminizes all genetic males, this feminization is not stable. When the hormone treatments were discontinued at metamorphosis and the little toads kept alive another three months, a high percentage of hermaphrodites and males was found. The hermaphrodites represent genetic males which, after the cessation of treatments, revert to males (table 1). Isolated testicular islands developed in the medullary region of such hermaphrodite glands (fig. 9). In these islands cytologic differentiation is more advanced than in the testes of controls of the same age. Maturation stages appear in some of the islands, while the testes of controls still contain only spermatogonia.

High concentrations of estradiol (500 to 1000 $\mu\text{g}/\text{l}$) retard gonad development. At the time of metamorphosis, the sex glands are so poorly developed that identification of the sexes is impossible. However, the results obtained from the thyroprivic lots, 500 b and 1000 b, indicate that the feminizing effect of estradiol diminishes as the hormonal concentration increases (table 1). Small but structurally normal testes and ovaries are found at the dosage of 1000 $\mu\text{g}/\text{l}$ (figs. 10, 11) and sex distribution shifted in the male direction. Evidently high levels of estradiol fail to feminize the genetic males.

Adrenal enlargement as produced in frog larvae by estradiol treatments is also observed in the toad. After osmication by fixation in Flemming's fluid, the adrenal cortical cells appear

black (fig. 12). The adrenal tissue is increased in mass and its ventrolateral descent delayed.

3. *Larvae treated with methyltestosterone.* Although methyltestosterone is the most potent masculinizing hormone in *Rana* tadpoles (minimum dose 0.01 $\mu\text{g/l}$, Witschi, '50), it does not masculinize the gonads of toads, whether given only before metamorphosis or continuously over extended periods. At concentrations of 20 to 50 $\mu\text{g/l}$, animals autopsied at metamorphosis show equal numbers of males and females (table 1). Of 106 animals examined (sterile animals excluded), 48 are males, 6 hermaphrodites and 52 females. For assurance of better gonadal differentiation, most of the animals were preserved a few weeks after discontinuation of the hormone treatments. Normal testes and ovaries are seen in these groups (figs. 13, 14). The same is also true for the thyroprivic animals which were treated continuously over 4 months with a dosage of 20 $\mu\text{g/l}$ and preserved after a hormone-free period. The occurrence of a few hermaphrodites is not uncommon also in controls, at this early stage.

Complete or partial sterilization occurs in the groups receiving continued treatment of methyltestosterone at the concentration of 50 $\mu\text{g/l}$. Fewer germ cells are present (fig. 15). However, the testes or ovaries regenerate if the hormone treatment is suspended and a short time is allowed for the gonad to grow (figs. 16, 17).

High concentration of methyltestosterone, 500 $\mu\text{g/l}$, further inhibits the growth of the gonads. At the time of metamorphosis, these gonads are small and not differentiated. The thyroprivic tadpoles of this dosage level died accidentally.

Precocious development of secondary sex characters occurs in methyltestosterone-treated groups. As soon as the animals complete metamorphosis, the forearms enlarge and the dark pigmentation of the throat, as characteristic of sexually mature males, become clearly noticeable in both sexes. Androgen must enter the larval body as freely as estrogen.

B. The development of the cortical lobe

The structure in question is often designated as "Bidder's organ." In the discussion it will be explained why the author gives preference to the term *cortical lobe*.

Methyltestosterone retards the growth of the cortical lobe in both intact and thyroprivic animals, but does not suppress the differentiation of its ovarian characteristics (fig. 18). The lobes of controls are consistently larger (fig. 19). Continued androgenic treatments produce no further drastic effects; the number of ovocytes remains low; and the stroma is relatively increased (fig. 20). Following cessation of hormone treatments, the growth of the lobes is rapidly resumed.

Estradiol likewise reduces the size of the cortical lobe, though less than methyltestosterone. No indication of stimulation is ever noticed. Histologically the lobes are closer to normal structure than those of the testosterone series (compare figs. 21 and 20 with 22). The increase of the stroma in the testosterone series seems related to ovocyte degeneration. Apparently the granulosa cells survive longer than the germ cells.

C. The effects of hypophysectomy on sex differentiation

The hypophyseal analage was removed at the late neurula stage. Six male and 4 female hypophysectomized tadpoles were preserved at the age of 150 days. Initial sex differentiation and early gonadal development appear unaffected. However, testicular development is retarded in comparison to controls of same age. The ovaries and cortical lobes are normal (fig. 23). Oviducts are absent in both thyroidectomized and hypophysectomized animals regardless of age.

DISCUSSION

The analysis of hormonal effects on sex differentiation in toads is rendered difficult by incompleteness of sex differentiation at the metamorphosis stage. Thyroidectomy, preventing metamorphosis was helpful in obtaining more ad-

vanced stages of gonad development. Obviously the thyroid is without effect on the development of the gonad and germ cells at early stages. Our observations confirm earlier reports by Allen ('18) and Swingle ('18).

Since at certain levels estradiol feminizes the genetic males, while testosterone at all dosages fails to masculinize the genetic females, an interesting physiologic relationship is brought into evidence which links *Bufo* with the more primitive anurans. In general, amphibians may be separated into three categories according to their reactions to androgens, as follows: (1) masculinization of the genetic females, as in *Rana* and *Hyla*; (2) feminization of the genetic males, as in *Ambystoma* (Bruner and Witschi, '54) and *Pleurodeles* (Mintz and Gallien, '54); (3) without sex reversal, as in *Discoglossus* (Gallien, '50) *Alytes* (Witschi, '51) *Xenopus* (Witschi and Allison, '50; Witschi, '50) and *Bufo*. The mechanisms of these divergent responses to crystalline androgens are difficult to understand. However, present information about the genetic determination of sex in amphibians suggests a possible relationship between female monogametic constitution (XX) and positive masculinization response. Through the breeding experiments of Crew ('21) and of Witschi (rev. '29) it was established that in *Rana* the female sex is monogametic. On the other hand in *Ambystoma* (Humphrey, '45), *Pleurodeles* (Gallien, '54), *Xenopus* (Chang and Witschi, '55), and in *Bufo* (Ponse, '41; Witschi and Chang, '54), the females are digametic (ZW). Ovaries seem to respond to administered androgens if they are of homozygous constitution. This result is significant in view of the fact that heterozygous ovaries do transform into testes, namely under the conditions of testicular implantation (Witschi, '39; Humphrey, '42; Chang, '53), it must be concluded that the androgenic steroids are not identical with the effective agents under the conditions of the latter experiments.

The instability of feminization of estradiol-treated males of *Bufo* resembles analogous observations by Gallien ('44) for *Rana* and by Dantchkoff for the cock ('36). In these

species estradiol inhibits the medullary inductor without completely or permanently suppressing it.

From both histologic and physiologic viewpoints the term "Bidder's organ" seems to be misleading. The structure in question is not an independent organ and has no particular function; it simply is an upper cortical lobe of the gonad (Witschi, '33). Moreover it was not Bidder but Roesel von Rosenhof (1758) who first described this peculiar structure in toads, about 88 years before Bidder's publication (1846). After ablation of the testes of the male or of the ovaries of the female, it resumes growth and produces eggs which after fertilization may develop normally (Harms, '21; Guyénot and Ponse, '23). The results of the reported experiments on hormone treatments show that the lobe is incapable of testicular differentiation under any conditions. This conclusion is particularly supported by the group receiving the highest dosage of estradiol. While the sex ratio based on the differentiation of the main gonad shifts in the male direction the ovarian nature of the cortical lobe remains unchanged. The purely cortical nature of the structure appears now fully established and beyond possible doubts.

Contrary to the report of Talluri and Padoa ('53), no development of medullary cords in the cortical lobe was observed in the present series of experiments. According to Witschi ('33, p. 492) medullary rudiments are quite frequently found (20%) in the cortical lobes of normal males of *Bufo viridis*, the species used by the Italian authors. This peculiarity of their material may explain the difference in our observations.

The observed adrenal enlargement and the delay of ventrolateral descent resemble the case of *Rana* as reported by Segal ('53). As shown by Chang and Witschi ('55), this adrenal response leaves the sexual differentiation of the gonads unaffected.

The observations on the effect of hypophysectomy on the development of the gonads are in full agreement with the results reported in salamanders (Witschi, '30) and in frogs

(Chang and Witschi, '55). The initial differentiation of ovaries and testes remains unaffected and only at advanced juvenile stages a gradual retardation in growth and germ cell differentiation appears.

SUMMARY

1. In this study of sex differentiation under prolonged treatments with androgens and estrogens, thyroidectomy was performed in order to prevent metamorphosis. Allen's observation that removal of the thyroid gland has no effect on the early development of sex in amphibian larvae is fully corroborated.

2. Estradiol feminizes the genetic males at a concentration of 100 $\mu\text{g/l}$ of aquarium water; but the ovaries and testes are nearly normal in another group receiving 1000 $\mu\text{g/l}$. Adrenal hyperplasia occurs at this high dose.

3. Methyltestosterone causes neither masculinization nor feminization of gonads in the toads at any tested dosage levels. In both sexes the gonads are reduced in size, in proportion to dosage and duration of treatments.

4. The cortical lobes are reduced in estrogen- and androgen-treated animals, but particularly in the latter. Their ovarian cortical nature is always retained.

5. Hypophysectomy has no effect on embryonic sex differentiation. However, it retards the testicular and ovarian development at a later stage, beginning about three months after metamorphosis.

6. Types of hormone response among taxonomic groups of amphibians are compared and discussed. A possible relationship between the pattern of sex genotype and hormone response is suggested.

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PLATES

PLATE 1

EXPLANATION OF FIGURES

- 1 Cross section through testis of control at metamorphosis stage (35 days). $\times 100$.
- 2 Cross section through ovaries of control at metamorphosis (35 days). $\times 100$.
- 3 Section through testis of control toad (145 days). $\times 100$.
- 4 Section through ovary of control toad (145 days). $\times 100$.
- 5 Section through testis of thyroprivic tadpole (140 days). $\times 100$.
- 6 Section through ovary of thyroprivic tadpole (140 days). $\times 100$.
- 7 Section through hermaphrodite gonad of thyroprivic tadpole, treated with $100\text{ }\mu\text{g}$ estradiol/l, for 120 days. Note cortex at distal end of gonad and formation of ovogonial nests. $\times 100$.
- 8 Section through hermaphrodite gonad of another tadpole from same group as above. $\times 100$.

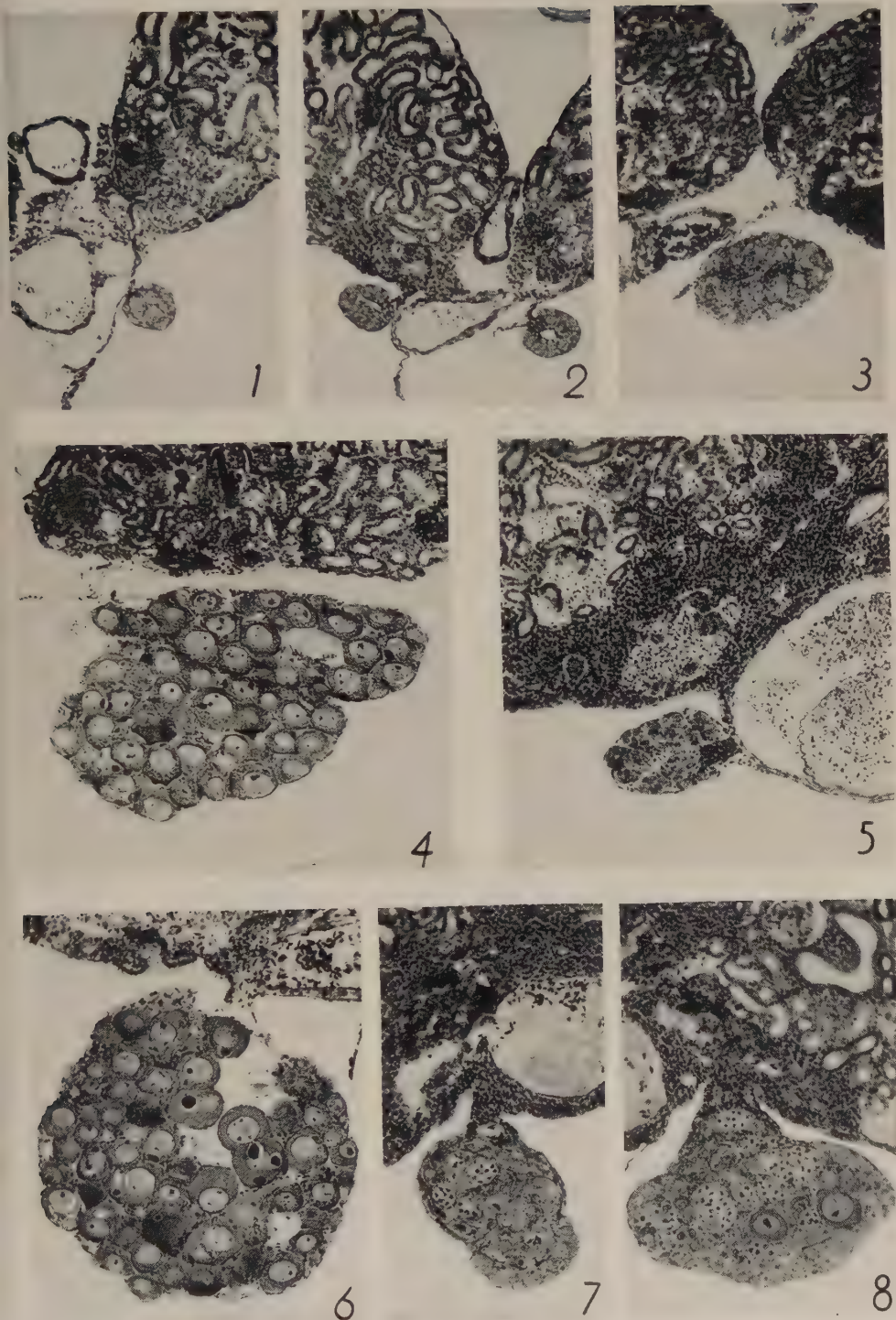


PLATE 2

EXPLANATION OF FIGURES

- 9 Cross section through gonad preserved 90 days after discontinuation of hormone treatment at metamorphic stage. Note the appearance of testicular islands. $\times 100$.
- 10 Section through testis of thyroprivic tadpole exposed to $1000\text{ }\mu\text{g}$ estradiol/l for 125 days. $\times 100$.
- 11 Section through ovary of thyroprivic tadpoles from the same group as above. $\times 100$.
- 12 Cross section through adrenals of thyroprivic tadpole, treated with $500\text{ }\mu\text{g}$ estradiol/l for 120 days. Adrenal cortical cells appear black; osmic preparation. $\times 100$.
- 13 Section through testis of toad three weeks after metamorphosis, treated with $20\text{ }\mu\text{g}$ methyltestosterone/l. $\times 100$.
- 14 Section through ovary of toad from same group as above. $\times 100$.
- 15 Section through nearly sterile gonad of thyroprivic tadpole, treated with $50\text{ }\mu\text{g}$ methyltestosterone/l for 120 days. The gonad consists of a center core of blastema and an efferent tubule located at the hilar region. $\times 100$.
- 16 Section through regenerating testis from some group as above, but preserved two months after cessation of treatment. $\times 100$.
- 17 Section through regenerating ovary from same group as case in figure 16. $\times 100$.
- 18 Section through cortical lobe at metamorphosis, treated with $50\text{ }\mu\text{g}$ methyltestosterone/l. $\times 100$.
- 19 Section through normal cortical lobe at metamorphosis. $\times 100$.

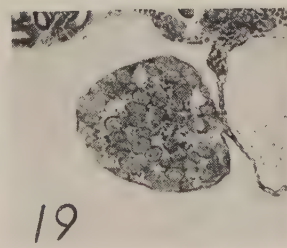
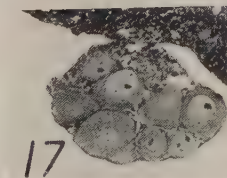
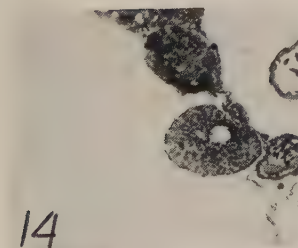
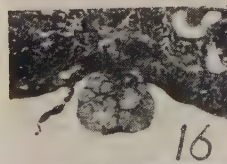
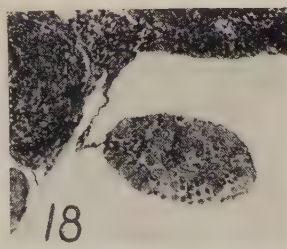
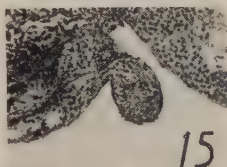
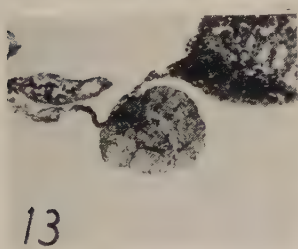
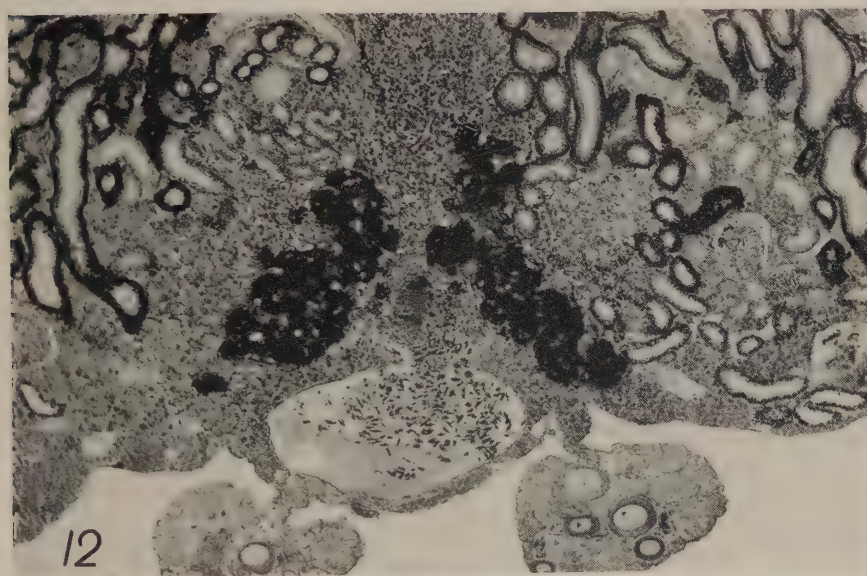
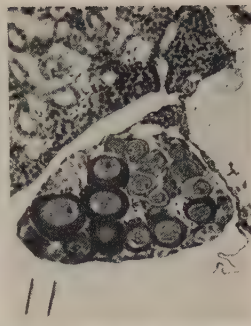
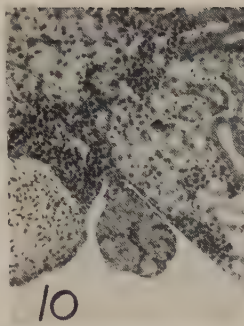
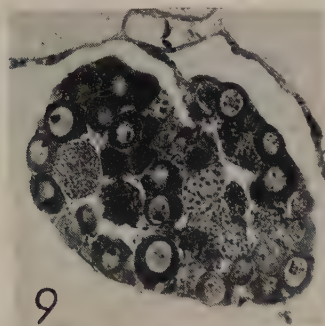
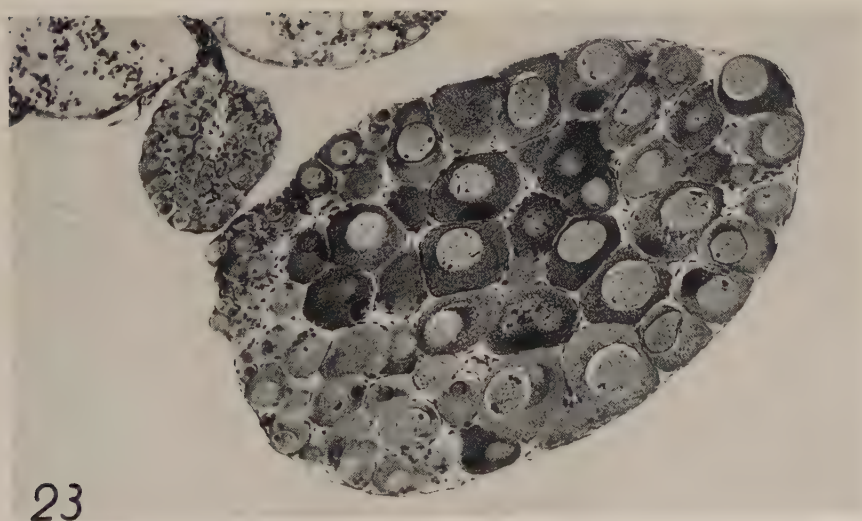
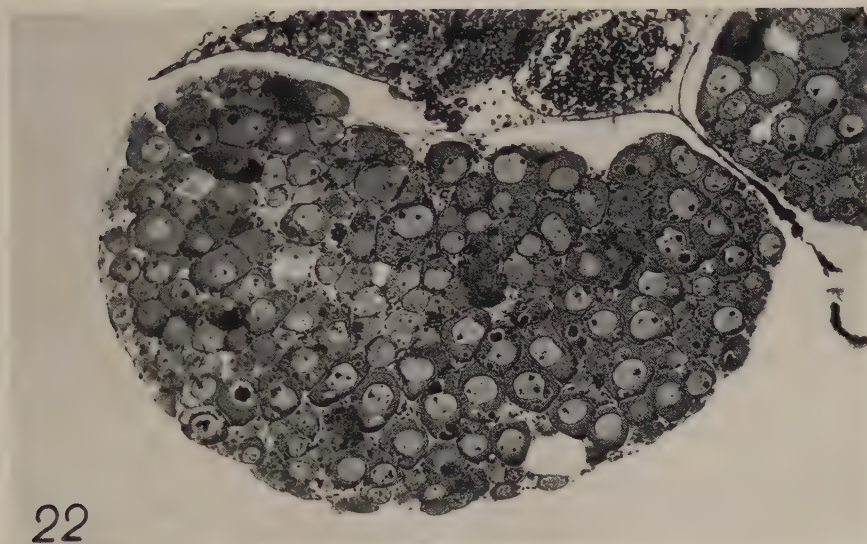
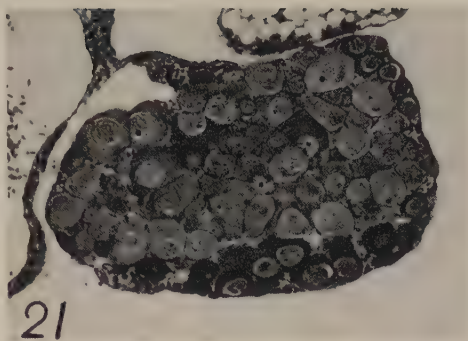
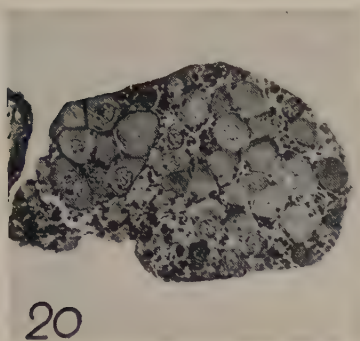


PLATE 3

EXPLANATION OF FIGURES

- 20 Section through cortical lobe of thyroprivic tadpole, treated with 50 μ g methyl-testosterone/l for 120 days. $\times 100$.
- 21 Section through cortical lobe of thyroprivic tadpole, treated with 1000 μ g estradiol/l for 130 days. $\times 100$.
- 22 Section through cortical lobe of thyroprivic control (135 days). $\times 100$.
- 23 Section through cortical lobe and part of ovary of hypophysectomized animal (150 days). $\times 100$.



A STUDY OF PITUITARY-THYROID RELATIONS IN IMMATURE RATS

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SIX FIGURES

INTRODUCTION

Although certain facets of the reciprocal relation between the pituitary and thyroid glands of adult vertebrates have been explored extensively, only scant attention has been paid to the fluctuations in synthesis, release and storage of the thyroid stimulating hormone (TSH) and the response of the thyroid gland to TSH in the developing animal. A few investigators have studied the structural alterations in the thyroid or pituitary gland of young animals (Jackson, '16; Cooper, '25; Smith and Starkey, '40; Bronks, '45; Rasmussen, '47), and some have attempted to interpret the thyroid changes in terms of the variations in the thyroid stimulating potency of the pituitary gland (literature reviewed by Adams, '46). There are, however, no reported systematic age studies correlating the morphologic changes in these glands with the amount of TSH released into the blood stream and the level of the circulating thyroid hormone. With the introduction of the stasis (starved non-metamorphosing) tadpole method of assaying TSH and the thyroid principle simultaneously in the circulating body fluids, a more complete elucidation of pituitary-thyroid interaction became possible (D'Angelo, Gordon and Charipper, '42; D'Angelo and Gordon, '50).

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In past investigations of pituitary-thyroid interaction usually only young maturing, adult or aging animals have been examined. It is surprising that the very young animal has been largely ignored since many critical changes occur at this time, i.e., in the case of the rat, a change from the poikilothermic to the homeothermic state at about 8 days (Jailer, '49), the establishment of secondary centers of ossification by 10 days (Scow and Simpson, '45), and the opening of the eyes at 14 to 15 days of age.

The object of this study has been to assay and to correlate the quantity of TSH in the pituitary gland with that found in the circulating blood during the first 15 days in the life of the rat. The presence of the circulating thyroid principle and the functional state of the donor rat's thyroid gland as indicated by histological examination were other parameters investigated.

MATERIALS AND METHODS

A total of 324 hooded rats, 1 to 15 days of age, from a closely inbred, modified Long-Evans strain, were utilized for this study. The serum, assayed for its thyroid hormone and TSH content, was obtained in all cases without treatment by chemicals or submission to fractionation procedures. The rats were decapitated, the blood pooled according to groups, centrifuged and stored in sterile vials in the freezing compartment of the refrigerator.

The pooled pituitaries from the same groups of rats were reduced to a homogeneous pulp, and a stock preparation of pituitary suspension (100 mg %) was prepared by adding 1 ml sterile amphibian saline (0.70% NaCl) to each milligram of pituitary. Injections were made either directly from this stock solution or from a more diluted preparation obtained by adding 1 ml of stock solution to 9 ml sterile amphibian saline (10 mg % pituitary suspension).

The sera and glands were assayed for TSH potency in tadpoles according to the method of D'Angelo, Gordon and Charipper ('42). Six tadpole heads were selected for histo-

logical study from each experimental group, and a total of 450 to 600 cell heights were averaged in order to ascertain the potency of any one specific material injected. The donor rats' thyroids were pooled according to the group studied, and sectioned and examined as a group. A total of 100 to 200 acinar cells were selected at random from each group and their heights measured. The data obtained in this study were appraised by Fisher's *t* test. *P* values of less than 0.05 were considered significant.

RESULTS

A. Histology of thyroid glands of 1- to 15-day-old rats

1. *Two to 4-day-old male and female rats.* The thyroid glands of all 2- to 4-day-old rats appeared differentiated but the female gland contained larger follicles, more colloid, and exhibited significantly greater ($P < 0.01$) average cell heights than the males (table 1; figs. 3 and 4). The blue-staining colloid in the peripheral follicles of the female gland displayed vacuolization and signs of resorption, while the inner follicles contained red-staining colloid or red tinged with blue. In contrast, more of the peripheral follicles as well as the more centrally located ones stained red in the male gland.

2. *Seven- to 9-day-old male and female rats.* Capsular connective tissue, follicular size, compression of lobules, and the amount of colloid were increased in this group. All the colloid stained blue in the female glands, but in the male glands there remained some red staining colloid, or red with a blue periphery. Droplets which took the same stain as the colloid were present in the female glands, but were more numerous in the cytoplasm of the male thyroid cell. These droplets were round, of different sizes, and occurred in varying numbers within the acinar cell. They were usually located between the nucleus and apical border of the cell. No sex difference in thyroid cell height was noted (table 1).

TABLE 1

General data for donor rats

EXPERI- MENT NO.	NO. OF RATS IN GROUP	AGE, SEX	MEAN BODY WT.	MEAN PIT WT.	MEAN THYROID CELL HT. $\pm$ S.E. ¹
			<i>gm</i>	<i>mg</i>	μ
25	44	1-3 days M and F		1.0 (estim.)	
34	10	1-3 days M and F	6.4	0.63	
36	30	2-4 days F	7.4	0.72	9.9 $\pm$ 0.10
37	33	2-4 days M	7.4	0.73	8.3 $\pm$ 0.07
35	12	5-8 days M and F	10.2	0.78	
49	23	7-9 days F	12.1	0.85	8.6 $\pm$ 0.08
50	51	7-9 days M	12.9	0.95	8.3 $\pm$ 0.10
55	9	11 days M and F	15.1	0.97	9.7 $\pm$ 0.08
48	26	11-12 days F	21.2	1.35	9.6 $\pm$ 0.08
47	26	11-12 days M	21.2	1.36	9.4 $\pm$ 0.10
58	16	14-15 days F eyes closed	18.0	1.23	9.9 $\pm$ 0.10
57	20	14-15 days M eyes closed	16.8	1.18	9.5 $\pm$ 0.09
56	19	14-15 days M and F eyes open	19.5	1.30	10.8 $\pm$ 0.10 (F) 10.2 $\pm$ 0.10 (M)

¹ Mean thyroid cell height $\pm$ standard error of the mean.

3. *Eleven- to 12-day-old male and female rats.* The gland increased in size, in vascularity, in number of colloid droplets and in cell height (table 1), but no sex differences were apparent. Some of the follicles were many times longer than wide which suggested that two or more follicles had combined to form one. The colloid of both male and female follicles stained red with blue peripheries.

The greatest change which occurred was the formation along the periphery of the lobe, limited by a lobule or plate within the lobe (fig. 5), of large blue-staining, irregularly shaped areas filled with colloid but having no definite cell walls. Floating in these "colloid lakes" were disintegrating acinar cells, pycnotic nuclei, interfollicular elements and red blood cells. One such area measured $144 \times 73 \mu$ at its widest diameter. The follicles surrounding such areas showed flattened epithelium, elongated nuclei and sometimes cellular debris in the center of the colloid.

4. *Fourteen- to 15-day-old male and female rats.* The peripheral follicles increased in size, contained marginal vacuoles in colloid or were devoid of colloid. A few thyroid "lakes" previously noted at 11 to 12 days were present. Huge irregularly shaped follicles were seen which appeared to be formed from the coalescence of about 6 to 8 follicles and contained many marginal vacuoles in the colloid. A study of serial sections revealed a large central area of colloid, more than 200μ long, whose outer walls consisted of small pockets complete with perifollicular connective tissue and interfollicular cells (fig. 6).

Finally, it may be seen from table 1 that when the eyes of the rats opened, a significant increase was noted in thyroid cell height.

B. Hormone content of pituitaries and sera of 1- to 15-day-old rats

1. *Presence of TSH in pituitary as indicated by increased tadpole thyroid cell heights.* An analysis of the data ob-

TABLE 2
TSH activity in pituitary glands of rats 1-15 days old

EXP.	AGE, SEX OF RATS	MEAN CELL HEIGHT INCREASE $\pm$ S.E. ¹					
		100 mg %			10 mg %		
		micra	%	P value ²	micra	%	P value
25	1-3 days M and F	..	..	..	—	—	< 0.30
36	2-4 days F	2.3 $\pm$ 0.07	33.8 $\pm$ 0.88	< 0.01	0.3 $\pm$ 0.05	4.4 $\pm$ 0.72	< 0.01
37	2-4 days M	2.7 $\pm$ 0.08	39.7 $\pm$ 0.88	< 0.01	0.6 $\pm$ 0.06	8.8 $\pm$ 0.88	< 0.01
49	7-9 days F	2.0 $\pm$ 0.07	31.2 $\pm$ 1.09	< 0.01	0.1 $\pm$ 0.05	1.5 $\pm$ 0.75	< 0.20
50	7-9 days M	2.5 $\pm$ 0.07	39.0 $\pm$ 1.10	< 0.01	1.3 $\pm$ 0.03	20.3 $\pm$ 0.47	< 0.01
55	11 days M and F	..	..	..	2.0 $\pm$ 0.07	37.7 $\pm$ 1.30	< 0.01
48	11-12 days F	2.6 $\pm$ 0.06	40.0 $\pm$ 0.90	< 0.01	1.0 $\pm$ 0.06	15.3 $\pm$ 0.92	< 0.01
47	11-12 days M	1.6 $\pm$ 0.06	24.6 $\pm$ 0.92	< 0.01	0.9 $\pm$ 0.06	13.8 $\pm$ 0.92	< 0.01
58	14-15 days F eyes closed	..	..	..	2.0 $\pm$ 0.05	37.7 $\pm$ 0.94	< 0.01
57	14-15 days M eyes closed	..	..	..	2.3 $\pm$ 0.06	43.3 $\pm$ 1.13	< 0.01
56	14-15 days M and F eyes open	..	..	..	1.6 $\pm$ 0.06	30.1 $\pm$ 1.12	< 0.01

¹ Mean cell height increase over saline-injected controls $\pm$ standard error of the mean.

² P values (Fisher's t test) of 0.05 or less are considered significant.

tained from assaying pituitary glands from rats 2 to 4 days of age (experiments 36 and 37) indicates that TSH was present in the gland at that time (table 2). It may be further noted that the glands from male rats were more potent than those from female rats.

When the rats reached 7 to 9 days of age (experiments 49 and 50), the 10 mg % pituitary suspension from female rats did not evoke a significant change in tadpole thyroid cell height when compared to the controls. It may be seen in table 2, however, that administration of the 100 mg % pituitary suspension of glands of both sexes resulted in significant increases. Three out of 6 tadpoles used for analysis of cell height increases received only 5 injections of the 100 mg % male pituitary suspension. Since by this time their fore limbs had erupted, no further injections were made.

TSH was detected at both dilution levels in glands from rats 11 to 12 days of age. At 14 and 15 days of age the eyes of some of the rats had opened (experiment 56). Injections of 10 mg % pituitary suspension from either female or male rats with their eyes closed resulted in significant increases in thyroid cell heights (table 2). Injections of pituitaries from 13 males and 6 females of the same age (experiment 56) but whose eyes had opened evoked smaller increases in cell heights (fig. 1). Since these assays were all carried out simultaneously, this represents a diminution in TSH content of the pituitary from animals whose eyes were open.

2. *Ability of pituitary to stimulate tadpole metamorphosis.* It may be seen from the results tabulated in table 3 that injections of 10 mg % pituitary suspensions from either male or female rats 1 to 8 days of age did not effect significant increases in tadpole hind limb lengths. Injections of the 100 mg % suspensions were effective.

A definite increased potency of the pituitary gland in the 7- to 9-day-old rats was evident from the induced speeding of the tadpole metamorphosis (fig. 2). With the 100 mg % suspensions the majority of tadpoles metamorphosed after the 5th injections, therefore rendering further injections un-

necessary. The emergence of forelimbs and tail resorption were criteria which superseded hind limb extensions and indicated that a definite increase in potency had occurred.

Injections of pituitary suspensions of female rats 14 to 15 days of age with their eyes closed were unable to increase the hind limb length significantly ($P < 0.10$), but significant increases were produced by male pituitaries and pooled pituitaries from male and female rats whose eyes were open.

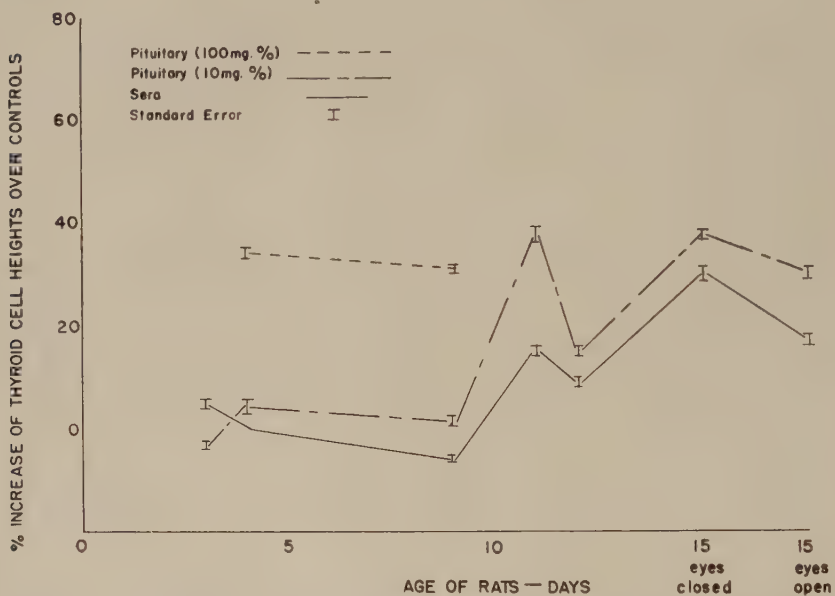


Fig. 1 TSH activity in pituitary glands and sera of female rats as indicated by increased tadpole thyroid cell heights.

3. *Presence of TSH in sera as indicated by increased tadpole thyroid cell heights.* The combined sera from female and male rats (1 to 3 days old) and the sera of 2- to 9-day-old female rats did not elicit significant increases in the tadpole thyroid cell height over those of the controls (table 4). Although the sera from male rats, 2 to 4 days old (experiment 37), produced a significant increase, no TSH could be detected in the sera of 9-day-old males.

At 11 to 12 days (experiments 47, 48 and 55) TSH was present in the sera in significant amounts. It was also detected in the sera of all rats 14 to 15 days of age, but a significant drop in the amounts of circulating TSH ($P < 0.01$) was associated with the opening of the eyes (fig. 1).

4. *Ability of sera to stimulate tadpole metamorphosis.* Although the pooled sera of 1- to 3-day-old male and female rats caused significant increases in hind limb lengths (table 4), the test was unable to detect circulating thyroid hormone

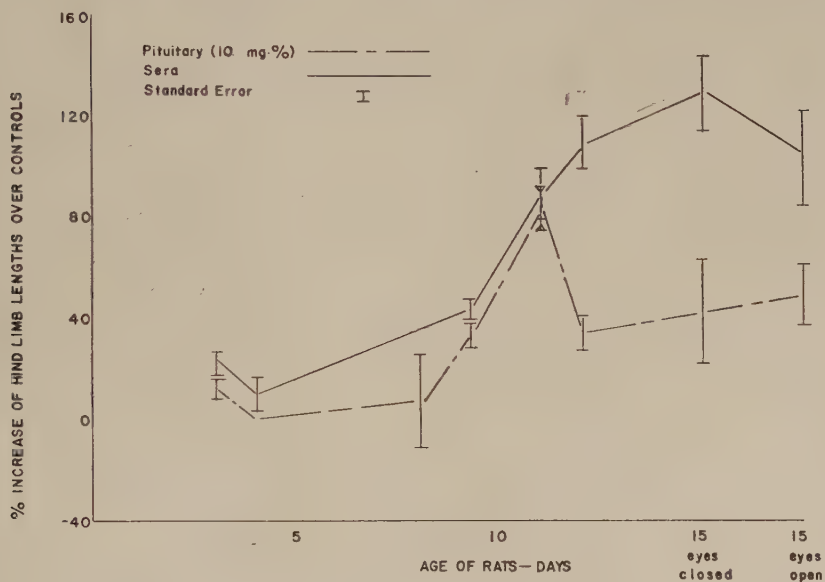


Fig. 2 Metamorphosis-stimulating activity of male pituitary glands and sera.

in the sera of female rats (experiment 36) or 2- to 4-day-old male rats (experiment 37) when assayed separately. Metamorphosis-stimulating activity was noted at 7 to 9 and at 11 to 12 days. At 14 to 15 days the sera was found to be more effective than the 10 mg % pituitary suspension in hastening metamorphosis (tables 3 and 4, fig. 2). Although the experimental tadpole hind limbs were increased to a significant degree above the control tadpole in each case, no one serum was superior in this ability.

TABLE 3
TSH activity in pituitary glands of rats 1-15 days old

EXP.	AGE, SEX OF RATS	MEAN HIND LIMB INCREASE $\pm$ S.E. ¹					
		100 mg %		10 mg %		P value ²	P value ²
		mm	%	mm	%		
25	1-3 days M and F	..	..	0.6 $\pm$ 0.26	11.5 $\pm$ 4.96	..	< 0.20
34	1-3 days M and F	1.5 $\pm$ 0.20	37.5 $\pm$ 5.00	0.0	0.0	< 0.01	0.0
36	2-4 days F	1.8 $\pm$ 0.22	45.0 $\pm$ 5.50	0.0	0.0	< 0.01	0.0
37	2-4 days M	3.3 $\pm$ 0.11	82.5 $\pm$ 2.75	0.0	0.0	< 0.01	0.0
35	5-8 days M and F	1.8 $\pm$ 0.33	45.0 $\pm$ 8.25	0.3 $\pm$ 0.10	7.5 $\pm$ 1.81	< 0.01	< 0.40
49	7-9 days F	All metamorphosed by 5 injections		1.3 $\pm$ 0.14	38.0 $\pm$ 4.10		< 0.01
50	7-9 days M	Preforelimbs and forelimbs by 3rd and 5th injections		1.2 $\pm$ 0.24	35.0 $\pm$ 7.00		< 0.01
55	11 days M and F	..	..	2.5 $\pm$ 0.26	83.3 $\pm$ 8.70	..	< 0.01
48	11-12 days F	Preforelimbs and forelimbs by 5th and 7th injections		1.8 $\pm$ 0.31	45.0 $\pm$ 7.75		< 0.01
47	11-12 days M	Prefore., forelimbs and tail resorp. by 5th and 7th inj.		1.4 $\pm$ 0.31	35.0 $\pm$ 7.70		< 0.05
58	14-15 days F eyes closed	..	..	1.6 $\pm$ 0.68	53.3 $\pm$ 22.40	..	< 0.10
57	14-15 days M eyes closed	..	..	1.3 $\pm$ 0.61	43.3 $\pm$ 20.30	..	< 0.02
56	14-15 days M and F eyes open	..	..	1.6 $\pm$ 0.36	53.3 $\pm$ 12.00	..	< 0.02

¹ Mean hindlimb increase over saline-injected controls $\pm$ standard error of the mean.

² P values (Fisher's t test) of 0.05 or less are considered significant.

TABLE 4

TSH and thyroid hormone activity in sera of rats 1-15 days old

EXP.	AGE, SEX OF RATS	MEAN CELL HEIGHT INC. $\pm$ S.E. ¹		MEAN HIND LIMB INC. $\pm$ S.E. ¹		P value ²
		micra	%	mm	%	
25	1-3 days M and F	0.3 $\pm$ 0.05	4.7 $\pm$ 0.70	1.3 $\pm$ 0.17	25.0 $\pm$ 3.26	< 0.01
36	2-4 days F	0.1 $\pm$ 0.05	0.0	0.6 $\pm$ 0.27	15.0 $\pm$ 7.30	< 0.50
37	2-4 days M	0.6 $\pm$ 0.05	8.8 $\pm$ 0.73	0.4 $\pm$ 0.31	10.0 $\pm$ 7.75	< 0.50
49	7-9 days F	— 0.4 $\pm$ 0.04	— 6.0 $\pm$ 0.60	2.2 $\pm$ 0.40	65.0 $\pm$ 11.80	< 0.01
50	7-9 days M	— 0.4 $\pm$ 0.05	— 6.0 $\pm$ 0.75	1.5 $\pm$ 0.16	44.0 $\pm$ 4.70	< 0.01
55	11 days M and F	0.8 $\pm$ 0.05	15.0 $\pm$ 0.92	2.7 $\pm$ 0.40	90.0 $\pm$ 13.40	< 0.01
47	11-12 days M	0.7 $\pm$ 0.06	10.7 $\pm$ 0.90	4.4 $\pm$ 0.48	110.0 $\pm$ 12.00	< 0.01
48	11-12 days F	0.6 $\pm$ 0.05	9.2 $\pm$ 0.77	3.5 $\pm$ 0.57	88.0 $\pm$ 14.3	< 0.01
58	14-15 days F eyes closed	1.6 $\pm$ 0.05	30.1 $\pm$ 0.94	3.6 $\pm$ 0.46	120.0 $\pm$ 15.30	< 0.01
57	14-15 days M eyes closed	1.2 $\pm$ 0.06	22.6 $\pm$ 1.10	2.9 $\pm$ 0.50	130.0 $\pm$ 16.60	< 0.01
56	14-15 days M and F eyes open	0.9 $\pm$ 0.05	16.8 $\pm$ 0.90	3.2 $\pm$ 0.57	106.6 $\pm$ 18.80	< 0.01

¹ Mean increase over saline-injected controls $\pm$ standard error of the mean.² P values (Fisher's t test) of 0.05 or less are considered significant.

DISCUSSION

New born animals

Examination of the data (tables 2 and 3) indicates that the 10 mg % pituitary suspensions from rats 2 to 4 days of age contained enough TSH to induce an increase in thyroid cell height in the assay animal, but were unable to accelerate tadpole metamorphosis. This, perhaps, may be attributed to the greater sensitivity of the thyroid cells to low levels of TSH as compared to the hind limb response.

The sex difference in TSH potency of the pituitary, found to exist in the present experiments (tables 2 and 3) has been reported also by Adams and Mothes ('45) in mice, by Turner and Cupps ('39) in rats, by Bates, Riddle and Lahr ('35) and by Reece and Turner ('37) in cattle. No sexual difference in pituitary TSH, however, was reported in rabbits by Ch'en and Van Dyke ('36) and Saxton and Greene ('39), Bergman and Turner ('41) or in the pituitaries and urine from human beings (Aron and Klein, '30; Müller, Eitel and Loeser, '35; Witschi and Riley, '40). At 2 to 4 days the male pituitaries at the two levels injected (100 mg %, 10 mg %) revealed significantly greater activity than the female glands. Associated with the greater TSH potency of the male gland was the presence of TSH in the sera (table 4). No TSH was detected in the sera of the female.

The histological study of the donor rats' thyroid glands yielded further information about the functional state of the thyroid. Both male and female glands were developed and contained follicles and colloid. It was anticipated that the newborn rat's thyroid would exist in a developed state, since there is evidence that the thyroid gland develops prenatally in most mammals and about the time of birth offers evidences of an ability to function (Kull, '26; Gorbman and Evans, '43; Hall and Kaan, '42; Vidovic, '51; Sethre and Wells, '51). This was not found to be true for the mouse according to Smith and Starkey ('40). The cell heights of the newborn female thyroid gland were statistically greater and more

active than the male's as judged by staining affinity, size of follicles and the amount of colloid. The larger peripheral follicles of the females usually stained blue and contained many marginal vacuoles which according to Leblond ('49) are features of stimulated glands.

The histology of the thyroid at any time actually reflects events which occurred at a previous time. The stimulated thyroid and the lower TSH potency of the pituitary from female rats, as compared to the males, may well represent a previous period of activity. It may also be true that female rats are releasing TSH in a concentration below the threshold level of the assay animal, and the hypertrophied cells may, therefore, represent a greater sensitivity to TSH for the thyroid of female animals. The greater TSH potency of the male pituitary, the presence of circulating TSH and the histological picture of a relatively unstimulated thyroid are indicative of a stage in which the thyroid has not as yet responded. In either case the thyroid glands are not capable of synthesizing or releasing an amount of hormone into the circulating system which is detectable by the assay method.

It usually has been assumed that the fluctuations of thyroid cell height could be interpreted in terms of the TSH released into the blood stream, while the TSH content of the anterior pituitary was indicative of a storage of TSH. According to this view, the lower thyroid cell heights and the greater potency of the pituitaries in the 2- to 4-day-old males, as compared with the females, would indicate greater storage of TSH for the males, and greater release of hormone in the females. The data obtained from this investigation, however, show that such an assumption may lead to erroneous conclusions. According to the assays of the sera by the stasis tadpole method, it is the 2- to 4-day-old males and not the females which are releasing TSH into the blood stream in any detectable amounts. This emphasizes the importance of assaying the circulating fluid for TSH before attempting any interpretation of the functional state of the pituitary gland, i.e., its rate of synthesis, release and storage of TSH.

Seven- to 9-day-old rats. The pituitaries of 7- to 9-day-old male rats have retained their superiority over the female gland in stimulating thyroid cell height. Only injections of the 100 mg % female pituitary suspensions produced significant increases in cell height over the controls while both concentrations (10 mg %, 100 mg %) of male pituitary evoked significant changes.

The ability of the pituitary glands to stimulate metamorphosis in the tadpole, however, did not follow this pattern. While the 10 mg % pituitary suspension obtained from females did not evoke an increase in thyroid cell heights, both the female and male glands at this concentration induced increments in tadpole hind limb lengths. This result was unexpected since the reaction of the cell heights was considered more sensitive than that of the hind limbs.

The recent work of Greer ('52), Gassner ('53) and Dobyns ('53) have suggested that more than one factor may be involved in TSH activity although Halmi et al. ('53) and Vanderlaan and Caplan ('54), among others, found it unnecessary to postulate a multiple-factor TSH. The possibility exists that the stasis tadpole assay method might discriminate between two factors with the increase in hind limbs a reflection of the iodine-purging or iodine-metabolic activity and the increase in cell height an expression of the growth factor. Any dichotomy of TSH action could then be explained by the independent variation of the two factors. Further investigation is necessary to determine the validity of such an interpretation.

The weaker pituitary suspension from 2- to 8-day-old rats, after 7 injections, produced moderate hind limb length increments (table 3), while the same suspension from 7- to 9-day-old animals stimulated metamorphic changes involving preforelimb formation, forelimb eruption, general body and pigmentation changes after only 5 injections. These effects may be interpreted to mean that the rat is now producing more TSH per gram of fresh pituitary tissue than it did at any earlier period. Variation in pituitary TSH with age

has been reported by other investigators (Adams and Mothes, '45; Reece and Turner, '37; Turner and Cupps, '39; Bergman and Turner, '41). This increase in TSH potency by the 9th day may coincide with the initiation of hypothalamic function since according to Jailer ('49) the albino rat changes from a poikilothermic to a homeothermic state at about the 8th day of life.

The sera of 7- to 9-day-old rats not only lacked TSH activity but actually appeared to depress the thyroid cell heights of the test tadpoles. Since no TSH was detected in the sera, the increase in tadpole hind limb lengths could be attributed only to the circulating thyroid principle present. Associated with this presence of circulating thyroid hormone was a decrease in the female rats thyroid cell size. An increase in the number of colloid droplets was noted in the acinar cells of the male thyroid.

Eleven- to 12-day-old rats. Administration of the 10 mg % and 100 mg % suspensions from both female and male pituitary glands produced significant increases in tadpole thyroid cell heights; the female glands were more potent than those from the males.

TSH was detectable also in the sera of the 11- to 12-day-old rats. The enhancement of tadpole metamorphosis produced by these sera was probably a reflection of the presence of both TSH and the thyroid hormone. No sexual difference could be detected in the metamorphic-stimulating potency of the sera. The increase in the cell heights of the donor rats' thyroids probably was the result of the TSH in the sera.

At this time there occurred a degeneration of the follicular walls within a lobule to form "colloid lakes." Jackson ('16) reported a similar phenomenon and Baillif ('37) correlated this degenerative state with thyroid stimulation. It is interesting to correlate the presence of hormone in the sera and the histological evidence of stimulation of the thyroid

gland with the increased demand for the thyroid hormone which occurs about this time. The rat is now able to maintain its body temperature (Jailer, '49) and, according to Scow and Simpson ('45), Scow, Simpson, Asling, Li and Evans ('49) and Noback, Barnett and Kupperman ('49) the secondary centers of ossification become established about 10 days after birth. Thyroid secretion has been found to influence these centers. These demands, along with others, may be responsible for the augmented release of TSH into the blood stream by the pituitary and for the increased amounts of circulating thyroid hormone.

Fourteen- to 15-day-old rats. It is at about this chronological age that the opening of the eyes is noted in the rat. The present results indicate that the opening of the eyes was correlated with a decrease in the TSH content of the pituitary. This was associated with a diminished quantity of circulating TSH, a result not expected if light was able to stimulate a release of TSH from the pituitary.

Despite this decrease in TSH potency in the pituitary and in the blood, increased activity of the thyroids of the rats was noted. It is possible that the opening of the eyes induced a sudden outpouring of TSH into the blood stream with the thyroid removing the hormone quickly from the blood stream which resulted in sudden hypertrophy. Such an interpretation assumes necessarily that this effect is very rapid. The specific time at which the blood was withdrawn and the pituitaries removed from the donor rat is important and must have occurred after the response of the thyroid and pituitary glands to the light. It is also possible to interpret the decrease in TSH potency of the pituitary gland as an inhibition by the light of the synthesis and release of this hormone from the hypophysis, but associated with an increased sensitivity of the thyroid gland to the hormone. The variations in sensitivity with age have been suggested by Belasco and Merlin ('41) in their studies on variations in thyroid tissue respiration. Regardless of which interpretation is more correct, the

general impression is gained that the pituitary and thyroid glands of rats are extremely labile.

SUMMARY

The functional relation between the thyroid and the pituitary in 1- to 15-day-old rats has been studied by assaying the quantity of TSH contained in the pituitary gland and the amount released into the blood stream by the stasis tadpole technique. The presence of the circulating thyroid principle was also ascertained as well as the functional state of the donor rats' thyroid as indicated by its histology.

The pituitaries of the young rats, 1 to 15 days of age, store relatively little TSH but synthesize and release their hormone into the blood at a fairly constant rate.

The thyroid gland (as indicated by its histology) and the pituitary (as indicated by assay data) are capable of functioning in 2- to 4-day-old rats.

A sexual difference exists with female rats often exhibiting a higher thyroid epithelium and the male rats a more potent pituitary.

An increase in the TSH concentration of pituitary tissue from both male and female rats occurs at 7 to 9 days of age. The sera of 7- to 9-day-old rats, although lacking in TSH, contain thyroid principle as evidenced by their ability to induce metamorphosis in the "stasis" tadpole.

TSH appears in the sera of the 11- to 12-day-old rats. At this time the "colloid lakes," large degenerating areas of thyroid follicles, are present in the thyroid lobes.

A diminution in TSH in both the pituitary and the sera occurs at the time of opening of the eyes. Concurrently with the opening of the eyes there is an increase in rat thyroid cell height and the appearance of large cavernous structures, apparently formed by the coalescence of follicles within a platelet.

It would appear that the pituitary and thyroid glands of immature rats are very labile, responding sensitivity to environment stimuli and metabolic demands.

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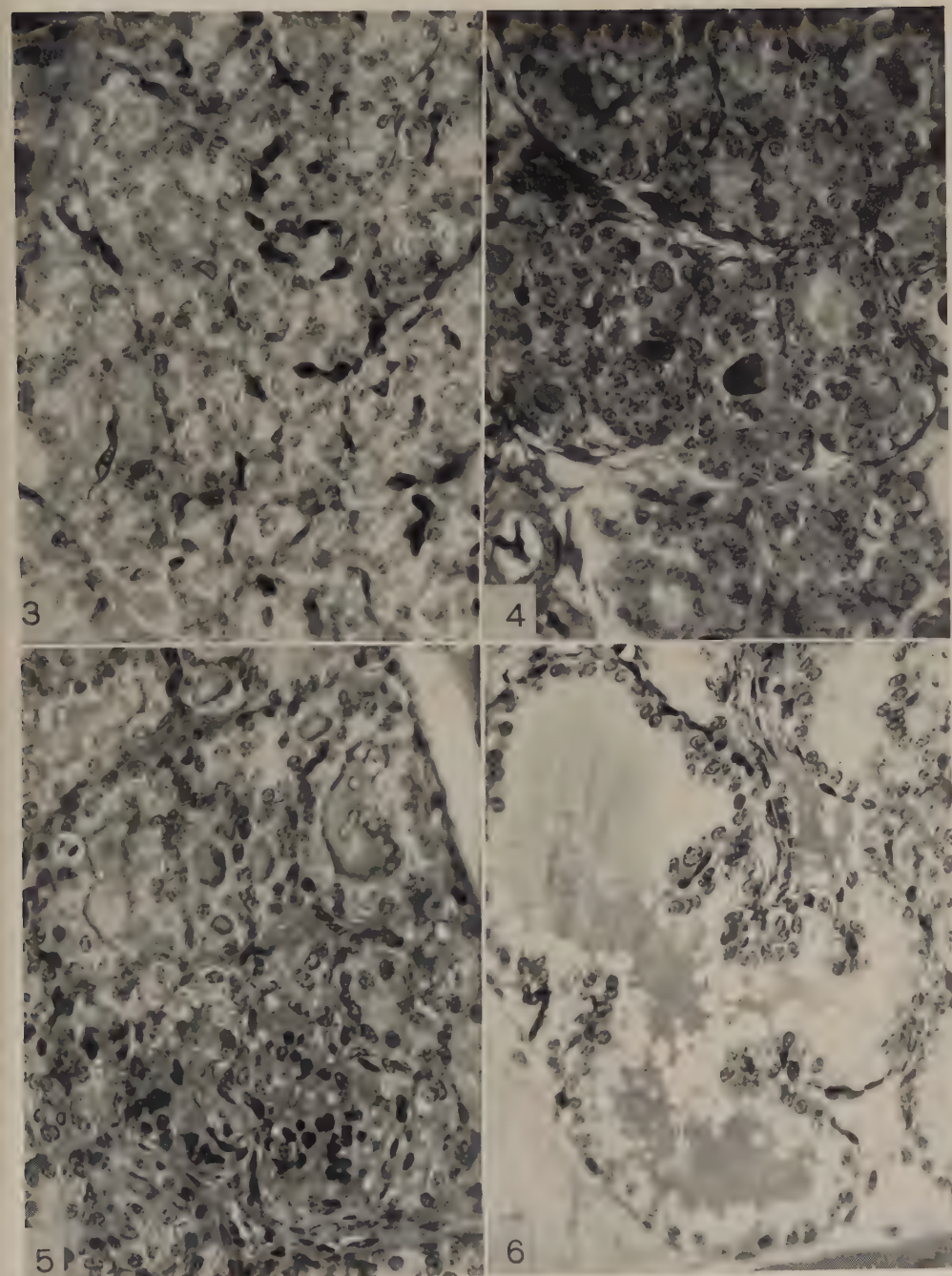
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PLATE 1

EXPLANATION OF FIGURES

Figures 3 to 6 are all photomicrographs of sections through the thyroid gland of normal untreated rats ($\times 485$; Bouin, Masson).

- 3 A section through the thyroid gland of a male rat, 2 to 4 days old, showing follicular size, amount of colloid, and presence of connective tissue.
- 4 A section through the thyroid gland of the female rat, 2 to 4 days old, demonstrating a more marked division of the gland into plates or lobules, larger follicles, and a greater amount of colloid than may be seen in the male gland.
- 5 A section through the thyroid gland of a 11- to 12-day-old female rat showing the degeneration of the follicles confined to one peripheral plate or lobule.
- 6 A section through the thyroid gland of a female rat, 14 to 15 days of age, showing a large cavernous structure which apparently was formed from the coalescence of at least 6 to 8 follicles.



COMPONENTS OF PERIARTERIAL EXTENSIONS OF CELIAC AND MESENTERIC PLEXUSES¹

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FOUR FIGURES

According to current concepts, the efferent components of the periarterial extension of the celiac, superior mesenteric and inferior mesenteric plexuses are postganglionic sympathetic fibers derived from the celiac and the superior and inferior mesenteric ganglia and preganglionic parasympathetic fibers that traverse these plexuses to reach parasympathetic ganglia in the biliary system, the pancreas and the gastro-intestinal tract. Ganglion cells, usually aggregated in small ganglia, in the nerves adjacent to the celiac and mesenteric arteries have been reported (Mitchell, '53), but adequate accounts of such ganglia and their distribution are wanting. Adequate fiber analyses of these nerves are also wanting. The present investigation has been undertaken to obtain additional data relative to the components of the periarterial extensions of the celiac and mesenteric plexuses, the frequency with which ganglia occur in them, and the anatomical relationships of these ganglia.

MATERIAL AND METHODS

In the initial phase of this investigation, studies were carried out to determine the relative frequency, size, and distribution of ganglia in the neural plexuses associated with the celiac and mesenteric arteries and their branches

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² Lederle Fellow, Summer, 1954.

in the rat, the cat and man. The arteries with the nerves and other tissues adjacent to them were fixed in 10% formalin. Each arterial system with the adjacent tissues was divided into portions that could be imbedded, sectioned longitudinally and mounted on 3×1.5 inch slides. The sections were cut to a thickness of 25μ , mounted serially and stained with hematoxylin and eosin. They were then examined for the presence of ganglion cells distal to the ganglia located in relation to the aorta and the proximal portions of the celiac and the superior and inferior mesenteric arteries. The locations of the ganglion cells observed were indicated as accurately as possible on diagrams of the arteries in question. Photomicrographs of areas of sections were prepared to illustrate the relative sizes of aggregates of ganglion cells and their relationships to the nerves adjacent to the arteries. In some instances ganglion cell counts were made.

In order to determine the relative frequency of preganglionic and myelinated afferent fibers in the proximal and the more distal portions of the neural plexuses in question, segments of the arteries and the adjacent nerves, taken at various distances from their origins, were stained with osmic acid for the demonstration of myelinated fibers and sectioned transversely. Other segments were sectioned transversely and stained according to Holmes' ('47) silver technic.

The distribution of the unmyelinated fibers in the nerves adjacent to the superior and inferior mesenteric arteries in the cat was also studied in longitudinal sections prepared by Holmes' silver technic. Some cats were subjected to surgical removal of the inferior mesenteric ganglia and allowed to live three weeks or longer after the operation to insure complete degeneration of the interrupted fibers. Osmic acid sections of the inferior mesenteric artery and the nerves adjacent to it taken transversely at various levels, following degeneration of the fibers interrupted by extirpation of the inferior mesenteric ganglia, were also studied for intact myelinated fibers.

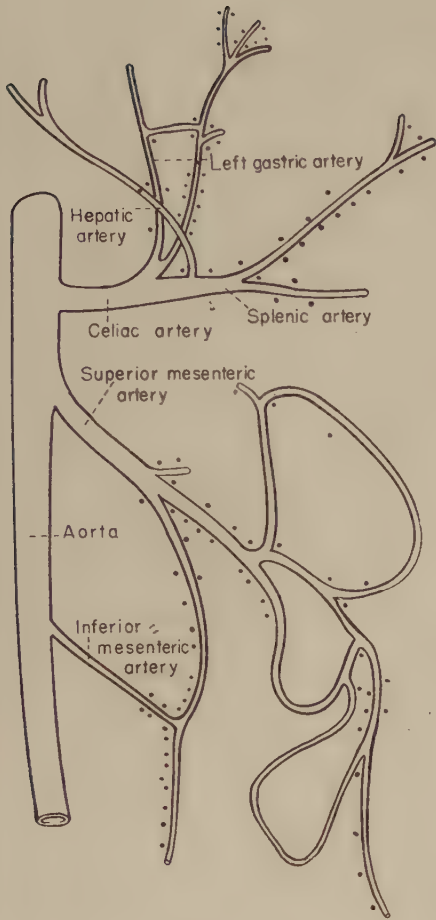


Figure 1

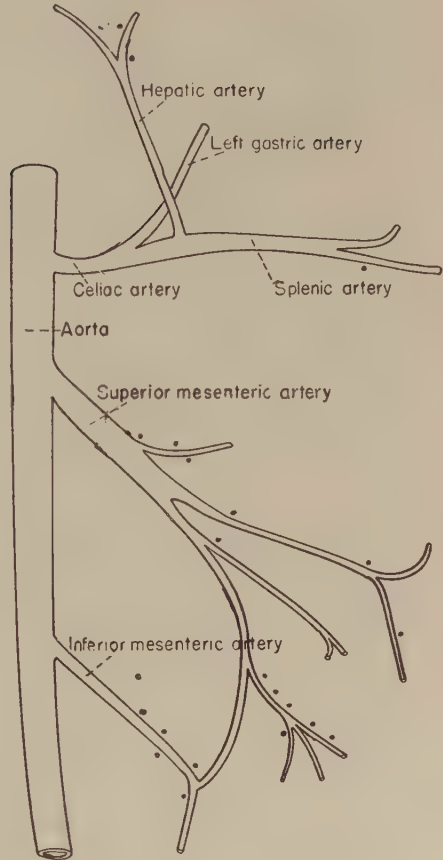


Figure 2

Fig. 1 Diagram to illustrate the approximate locations of ganglia observed in the neural plexuses that invest the branches of the celiac artery, the superior mesenteric artery and its branches and the inferior mesenteric artery and its branches, distal to the celiac, the superior mesenteric and the inferior mesenteric ganglia, in preparations obtained from a single rat.

Fig. 2 Diagram to illustrate the approximate locations of ganglia observed in the neural plexuses that invest the branches of the celiac artery, the superior mesenteric artery and its branches and the inferior mesenteric artery and its branches, distal to the celiac, the superior mesenteric and the inferior mesenteric ganglia, in preparations obtained from a single cat.

ANATOMICAL DATA

Ganglia in periarterial plexuses

In the rat ganglia occur frequently in the neural plexuses that invest the branches of the celiac artery and in those

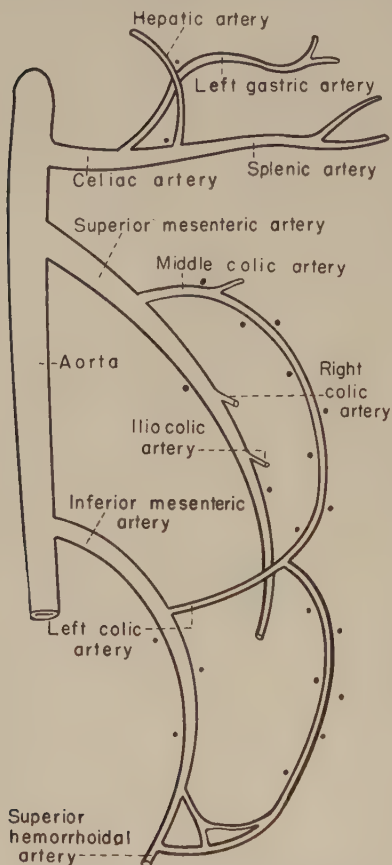


Fig. 3 Diagram to illustrate the approximate locations of ganglia observed in the neural plexuses that invest the branches of the celiac artery, the superior mesenteric artery and its branches and the inferior mesenteric artery and its branches, distal to the celiac, the superior mesenteric and the inferior mesenteric ganglia, in preparations obtained from the body of a child approximately two years of age.

that invest in the mesenteric arteries and their branches. Most of the ganglia that are located distal to the major ganglia of the celiac and the superior and inferior mesenteric plexuses include relatively few ganglion cells. Ganglia that include fewer than 25 ganglion cells each probably occur most frequently. Ganglia that include 25 to 100 ganglion cells each occur in abundance. Ganglia that include more than 100 ganglion cells each occur less frequently, but no less than 30 ganglia in this category have been observed in the periarterial plexuses in question in a single rat. The total number of ganglion cells in these plexuses, distal to the major celiac, superior mesenteric and inferior mesenteric ganglia, is very large.

Along the branches of the celiac artery, ganglia were observed chiefly adjacent to the left gastric and splenic arteries. Only a few were observed in relation to the hepatic artery. Along the superior mes-

enteric artery and its branches, ganglia were observed chiefly adjacent to the main arterial trunk and the proximal portions of the middle colic, right colic and ilio-colic arteries. A few small ganglia were also observed along the proximal portions of branches of the colic arteries. In the nerves adjacent to the inferior mesenteric artery and its branches, ganglia were observed along the entire course of the arterial trunk and along its ascending and descending branches. The distribution of ganglia along the major branches of the celiac artery and the trunks and major branches of the superior and inferior mesenteric arteries, observed in preparations from a single rat, is illustrated diagrammatically in figure 1.

In the cat the neural plexuses that invest the branches of the celiac artery and the trunk and branches of the superior mesenteric artery include relatively few ganglia distal to the celiac and superior mesenteric ganglia. In some of the cats examined no ganglia were observed along the branches of the celiac artery. In others a few small ones were observed along the left gastric and splenic arteries. Along the superior mesenteric artery and its branches a few small ganglia were observed adjacent to the proximal portion of the right colic artery and a few along more distal branches. In all the cats examined the plexus on the inferior mesenteric artery included one or more relatively large ganglia and one or more smaller ones, but relatively few ganglia were observed along the ascending and the descending branches of this artery. In most instances ganglia could be detected microscopically in the plexus around the inferior mesenteric artery. The distribution of ganglia along the branches of the celiac artery and the trunks and branches of the mesenteric arteries, observed in a single cat, is illustrated diagrammatically in figure 2.

In man, as observed in preparations obtained from full term fetuses and the body of a child approximately two years of age, the neural plexuses that invest the branches of the celiac artery and the trunks and branches of the mesenteric arteries exhibit ganglia in greater frequency than

the corresponding plexuses in the cat, but less frequently than those in the rat. A few small ganglia were observed in the plexus on the hepatic artery, but none were observed in those on the left gastric and splenic arteries. Two or more

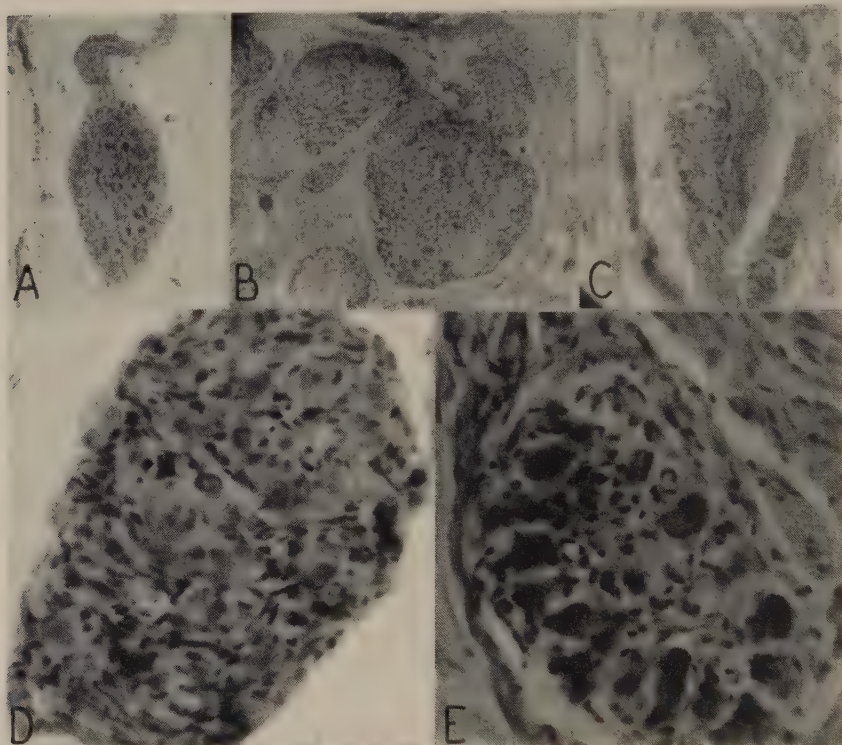


Fig. 4 A. Ganglion in the neural plexus investing the inferior mesenteric artery in a rat. B. Ganglion in the neural plexus investing the superior mesenteric artery (human). C. Ganglion in the neural plexus investing the inferior mesenteric artery (human). D. Ganglion in the neural plexus investing the inferior mesenteric artery in a cat. E. Ganglion in the neural plexus investing the inferior mesenteric artery (human).

small ganglia were observed adjacent to the proximal portion of the middle colic artery and one or more adjacent to the superior mesenteric artery near the origin of its right colic branch. In relation to the inferior mesenteric artery and its branches ganglia were observed along both the ascending

and descending branches of the left colic artery and distal to the origin of the left colic. The maximum number of ganglia observed along the inferior mesenteric artery and its branches was 17. Some of the more distal ones include no more than 10 to 35 ganglion cells each. Of the larger ones, usually 4 or 5 include in excess of 1000 ganglion cells each. The total number of ganglion cells in the nerves adjacent to the inferior mesenteric artery and its branches is relatively great as compared with the total number of ganglion cells in those adjacent to the superior mesenteric artery and its branches or the branches of the celiac artery. The distribution of ganglia along the branches of the celiac artery and the trunks and branches of the mesenteric arteries, distal to the major celiac, superior mesenteric and inferior mesenteric ganglia, as observed in preparations from the body of a child approximately two years of age, is illustrated diagrammatically in figure 3. Typical ganglia, as observed in the rat, the cat and man, are illustrated in figure 4.

Nerve fibers

Many preganglionic parasympathetic fibers of vagus origin that are concerned with the innervation of the gastro-intestinal tract, the biliary system and the pancreas traverse the celiac and superior mesenteric plexuses and their periarterial extensions. These plexuses are also traversed by afferent fibers of both the vagus and the splanchnic nerves. Most of their constituent fibers are postganglionic sympathetic fibers. Preganglionic sympathetic fibers to the ganglia that are located distal to the celiac and superior mesenteric ganglia also traverse them to reach the ganglia in which they terminate.

Transverse sections of the nerves adjacent to the proximal portions of the major branches of the celiac artery and those adjacent to the superior mesenteric artery in the cat, stained with osmic acid, exhibit myelinated fibers of relatively large caliber in small numbers and myelinated fibers of smaller

caliber in larger numbers, but the major portions of the sections are occupied by unmyelinated fibers. The largest of the myelinated fibers probably are afferent, but not all the afferent fibers are myelinated. The smaller myelinated fibers probably are chiefly preganglionic. Transverse sections of these nerves taken farther distally exhibit fibers in the same categories, but the large myelinated ones are somewhat less abundant. No diminution in the abundance of small myelinated fibers is apparent in most of the nerves. Since relatively few ganglion cells occur in these nerves in the cat, distal to the ganglia that are located in relation to the proximal portions of the celiac and superior mesenteric arteries, nearly all the preganglionic fibers traverse the entire lengths of the plexuses.

The nerves that extend distad from the inferior mesenteric ganglia along the inferior mesenteric artery include both large and small myelinated and unmyelinated fibers. They are derived chiefly through lumbar splanchnic, but in part through thoracic splanchnic and intermesenteric nerves. According to current concepts, parasympathetic preganglionic fibers of sacral origin reach the inferior mesenteric plexus through the hypogastric nerves to be conveyed to the colon through the plexuses investing the inferior mesenteric artery and its branches. This concept cannot be supported since no myelinated fibers remained intact in the superior hypogastric plexus caudal to the section following transection of the plexus near its junction with the inferior mesenteric plexus.

Transverse sections of the nerves adjacent to the distal portions of the inferior mesenteric artery or its branches exhibit small myelinated fibers in relatively smaller numbers than sections taken just distal to the inferior mesenteric ganglia. Many sympathetic preganglionic fibers obviously terminate in the ganglia in the periarterial plexuses.

Sections of the nerves adjacent to the mesenteric arteries and their branches prepared by Holmes' silver technic exhibit a preponderance of unmyelinated fibers. In the more distal sections the unmyelinated fibers make up a larger percentage

of the total number of fibers than in the proximal ones. On the basis of actual counts of the myelinated and the unmyelinated fibers in sections taken at various levels it is apparent that the unmyelinated ones become increasingly abundant in proportion to the myelinated ones from the proximal portions of the periarterial plexuses to the distal margin of the mesentery.

In sections of the nerves adjacent to the inferior mesenteric artery and its branches in the cat, taken after the fibers interrupted by surgical removal of the inferior mesenteric ganglia have undergone degeneration, only unmyelinated fibers remain intact. Such fibers are relatively more abundant in sections of the distal portions of the nerves than in those taken just distal to the inferior mesenteric ganglia. Many of the rami that enter the wall of the large intestine exhibit no evidence of nerve fiber degeneration except absence of myelinated fibers. The data obtained from sections taken after degeneration of the fibers interrupted by extirpation of the inferior mesenteric ganglia support the assumption that a large percentage of the postganglionic fibers in the neural plexuses along the inferior mesenteric artery and its branches is derived from ganglia incorporated in these plexuses and that afferent fibers enter these nerves chiefly at the level of the inferior mesenteric ganglia.

In man sections of the nerves adjacent to the branches of the celiac artery and the trunks and branches of the mesenteric arteries exhibit fibers that fall into the same categories as those in the corresponding nerves in the cat. Those of the nerves along the branches of the celiac artery afford no evidence of either a decrease in the percentage of small myelinated fibers or an increase in the percentage of unmyelinated ones from the proximal to the distal portions of the nerves. Those of the nerves along the superior mesenteric artery and its branches give evidence of an increase in the percentage of unmyelinated fibers from the proximal to the distal portions of the nerves.

Transverse sections of the nerves adjacent to the inferior mesenteric artery in man taken close to the aorta, stained with osmic acid, exhibit small myelinated fibers in percentages comparable to those observed in corresponding sections in the cat. The nerves that extend from the inferior mesenteric ganglia distad along the inferior mesenteric artery include large and small myelinated and unmyelinated fibers. In man, as in the cat, the inferior mesenteric ganglia receive preganglionic fibers chiefly through the splanchnic nerves. They are also traversed by preganglionic fibers that terminate in ganglia located in the periarterial plexuses farther distad and by afferent spinal nerve fibers. Sections of more distal parts of the nerves, as compared with proximal sections, show a marked percentage increase in the unmyelinated fibers. A large percentage of the postganglionic fibers in the distal portions of the nerves associated with the inferior mesenteric artery and its branches arises in ganglia that are located in the periarterial neural plexuses.

DISCUSSION

The data obtained in the present investigation show clearly that not all the ganglion cells concerned with the sympathetic innervation of the celiac, superior mesenteric and inferior mesenteric arteries and their branches and the organs to which they are distributed are incorporated in the ganglia that are located in relation to the proximal portions of these arteries. Many of them are located, either singly or in ganglia of varying sizes, in the neural plexuses that invest the arteries. Most of these ganglia lie adjacent to the blood vessels, but not within the adventitia. In general the ganglia that are located distal to those adjacent to the proximal portions of the arteries can only be observed microscopically. None were observed macroscopically except occasional ones along the inferior mesenteric artery. None were observed macroscopically in relation to the inferior mesenteric artery in the rat. In this animal, however, ganglia occur more

frequently in the periarterial plexuses throughout the entire area investigated than in the cat or man.

In both the cat and man ganglia occur much more frequently along the inferior mesenteric artery and its branches than along the branches of the celiac artery and the trunk and branches of the superior mesenteric artery. The ganglion cells that lie distal to the major ganglia located in relation to the proximal portions of the celiac and mesenteric arteries undoubtedly represent cells that have been displaced, during the course of development, from the primordia of the celiac, superior mesenteric and inferior mesenteric ganglia. The sources of the preganglionic fibers that make synaptic connections with the more distal ganglion cells undoubtedly are the same as those of the preganglionic fibers that make synaptic connections in the ganglia respectively that are located in relation to the proximal portions of the celiac and mesenteric arteries. The preganglionic fibers that reach the more distal ganglia traverse the corresponding plexuses. The perivascular plexuses in question, consequently, include many preganglionic sympathetic fibers in addition to the preganglionic parasympathetic fibers of vagus origin that traverse them to reach the ganglia in the enteric plexuses and the parasympathetic ganglion cells concerned with the innervation of the biliary system and the pancreas.

The preganglionic sympathetic fibers in the periarterial extensions of the celiac and superior mesenteric plexuses are chiefly components of the greater and lesser splanchnic nerves. Most of those in the perarterial extensions of the inferior mesenteric plexus are components of lumbar splanchnic nerves. This is in agreement with the findings of Harris ('43), in the cat, that most of the preganglionic fibers related to the inferior mesenteric ganglia reach them through rami that arise from lumbar segments of the sympathetic trunks. Both preganglionic and afferent splanchnic nerve fibers extend caudad from the celiac plexus to the inferior mesenteric and hypogastric plexuses. Some preganglionic fibers in this category traverse the inferior mesenteric ganglia to reach ganglia

located along the inferior mesenteric artery and its branches. In view of the frequency of ganglia along the inferior mesenteric artery and its branches and the relatively large sizes of some of them, it may be concluded that a large percentage of the postganglionic fibers concerned with the sympathetic innervation of the colon and the distal parts of the inferior mesenteric blood vessels are derived from ganglia that are located distal to the inferior mesenteric ganglia.

SUMMARY

In the rat, the cat and man the periarterial extensions of the celiac and the mesenteric plexuses along the celiac and the superior and inferior mesenteric arteries and their branches include numerous ganglia. In the cat and man ganglia occur more frequently and include larger numbers of ganglion cells in the periarterial extensions of the inferior mesenteric plexus than in those of the celiac and superior mesenteric plexuses. In addition to afferent, postganglionic sympathetic and preganglionic parasympathetic fibers, these plexuses include preganglionic sympathetic fibers that make synaptic connections in ganglia located in them. Consequently, the percentage of postganglionic fibers is greater and that of preganglionic fibers is less in distal than in the proximal portions of these plexuses. In view of the frequency with which ganglia occur in the periarterial extensions of the celiac and mesenteric plexuses, those distal to the major celiac and mesenteric ganglia need not be regarded as aberrant. The inclusion of ganglia probably represents an anatomical characteristic of these plexuses.

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A PHYSIOLOGICAL STUDY OF THE AMNIOTIC FLUID OF THE MOUSE

I. VOLUME AND WEIGHT CHANGES OF THE AMNIOTIC FLUID COMPARED WITH THE WEIGHTS OF FETUS AND PLACENTA DURING GESTATION ¹

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TWO FIGURES

INTRODUCTION

In connection with an experimental investigation regarding the habits of flow of amniotic fluid surrounding the fetal mouse, it became necessary to measure and record the daily changes in volume and weight of this fluid. Weighings of each fetus and the accompanying placenta were also performed at the same time. Previously very little information had been available concerning fluid changes in the smaller rodents and it was thought that this quantitative report might be an aid to others engaged in fetal rodent studies.

The mouse was the 9th and the smallest mammal to have its fetal amniotic fluid measured and recorded through the stages of gestation. Other observations of amniotic fluid volumes were found in the works of Paton et al. ('09) on the cow and sheep, Draper ('20) and Ibsen ('28) on the guinea-pig, Wolff ('09) and Lell ('31) on the rabbit, Wislocki ('35) on the cat and sow, Purdy and Hillemann ('50) on the hamster, and Monie ('53) on the human.

¹ A portion of a thesis approved as a partial fulfillment for the degree of Doctor of Philosophy, University of Pittsburgh, 1952. This work was aided by funds from the Department of Biological Sciences of which the author was a member.

MATERIALS AND METHODS

Young virgin female mice of the inbred, highly fertile "BAF" strain² were mated with males of the same strain at 10 P.M. followed by removal and examination at 8 A.M. The presence of a vaginal plug or sperm in the vagina indicated that copulation and possible conception had occurred and, upon confirmation, the female was isolated until the time designated for obtaining her litter.

The mice were raised and mated in a windowless, well-ventilated room under artificial light. Although a regular cycle of darkness existed during the 10 hours of mating, it was believed that the fetuses should be timed chronologically from the 8 A.M. examination rather than from the normally accepted 1-2 A.M. period (Snell et al., '40). The animals were kept at a temperature of $77 \pm 5^{\circ}\text{F}$. and received Purina Lab Chow Checkers and water ad libitum.

Beginning with the 10th day of gestation the pregnant mice were sacrificed daily until parturition, which was generally on the 20th day. Sacrificing was performed by manually parting the cervical vertebrae and this was followed by a ventral midline incision to allow the withdrawal of the horns of the uterus. The musculature of the exposed horns was separated between fetal swellings by means of fine iridectomy scissors and the intact amniotic sac containing the immersed fetus was manipulated free from the maternal tissue. Next, the amniotic sac was punctured at the point of least vascularity and the fluid was allowed to drop into a previously weighed microbeaker from which it was weighed. The volume was then measured with a 0.10 ml capacity pipette and readings to 0.01 ml were taken. The sac was separated from the fetus and placenta and these two structures were placed on filter paper for a half minute to absorb peripheral moisture. As the umbilical cord was detached from fetus and placenta and discarded a pinching-

² Obtained as weanlings from, and upon the advice of, the Roscoe B. Jackson Memorial Laboratory, Bar Harbor, Maine.

off of the cord prior to cutting prevented leakage of blood from both fetus and placenta.

Wet weights were then taken and recorded for the fetus and placenta. Weighings, recorded to 0.01 gm, were performed on a Roller-Smith precision balance of 150 mg capacity and a Torsion Balance of 120 mg capacity.

If the amniotic fluid escaped prematurely or became contaminated with vitelline blood, it was discarded and not used in the calculations. Furthermore, the data of pregnant animals which possessed fewer than 4 fetuses, placentas, or amniotic fluids were not included. Of a total of 53 litters examined, 36 litters met these numerical requirements and were recorded; 6 other litters comprising the 19th and 20th days of gestation were included despite the increased viscosity or even lack of fluid.

The fetus, placenta, and fluid contained in each amniotic sac were measured individually and an average of the measurements was obtained for each litter with the exception of the 10th and 11th days of gestation when the sac contents of a litter were measured together and the average obtained.

RESULTS

The data obtained from the 42 litters have been summarized in table 1. The weight of amniotic fluid was compared with the fetal and placental weights in figure 1, and the volume of amniotic fluid was plotted alone in figure 2.

Table 1 revealed that on the 10th day of gestation the average weights of fetus, placenta, and fluid were almost identical — 0.01 gm; whereas on the 20th day, the mean weight of fetus has reached 1.20 gm; placenta 0.70 gm; and the amniotic fluid was too viscous to measure or lacking altogether. The specific gravity was calculated and presented but the appreciable quantity and the alternating rise and fall seemed to indicate that further work would be necessary to confirm these figures. However, by smoothing the distribution, a general trend toward a low figure of 1.020 gm/

TABLE 1

Quantitative development of fetus, placenta, and amniotic fluid during gestation

DAY OF GESTATION	MATERNAL MOUSE	FETUS		PLACENTA	AMNIOTIC FLUID		
		Number present	Average weight	Average weight	Average weight	Average volume	Daily specific gravity
	<i>no.</i>		<i>gm</i>	<i>gm</i>	<i>gm</i>	<i>ml</i>	<i>gm/ml</i>
10	101	7	0.011	0.009	0.011	0.010	
	91	8	0.009	0.005	0.011	0.011	1.047
11	107	8	0.040	0.041	0.041	0.037	
	90	9	0.029	0.029	0.032	0.030	
	99	7	0.041	0.038	0.034	0.028	
	100	8	0.041	0.036	0.031	0.029	1.112
12	55	9	0.062	0.042	0.045	0.042	
	6	8	0.058	0.048	0.046	0.045	
	27	7	0.080	0.072	0.052	0.050	
	96	10	0.091	0.086	0.066	0.068	1.020
13	21	9	0.136	0.076	0.072	0.067	
	20	7	0.117	0.063	0.059	0.055	
	84	7	0.132	0.074	0.062	0.061	
	83	9	0.143	0.092	0.060	0.055	1.063
14	62	8	0.264	0.093	0.089	0.083	
	28	7	0.265	0.087	0.085	0.080	
	89	9	0.230	0.092	0.090	0.086	
	88	7	0.209	0.100	0.077	0.077	
	65	5	0.250	0.084	0.090	0.088	
	59	9	0.285	0.093	0.100	0.094	1.045
15	85	11	0.423	0.096	0.137	0.135	
	3	6	0.382	0.083	0.125	0.122	
	82	7	0.462	0.115	0.096	0.095	
	46	9	0.398	0.107	0.098	0.095	1.020
16	86	8	0.650	0.113	0.118	0.092	
	54	10	0.551	0.099	0.127	0.119	
	8	7	0.616	0.083	0.122	0.114	
	42	7	0.591	0.101	0.063	0.051	1.143
17	68	8	0.817	0.116	0.075	0.042	
	61	8	0.738	0.104	0.113	0.110	
	64	10	0.819	0.085	0.070	0.062	
	58	8	0.796	0.108	0.099	0.095	1.155
18	109	5	0.946	0.101	0.084	0.064	
	67	8	0.852	0.105	0.092	0.070	
	45	5	0.947	0.117	0.073	0.054	
	13	8	0.884	0.101	0.069	0.058	1.292
19	115	5	1.159	0.079	Measurements discontinued		
	116	7	1.124	0.077			
	76	6	1.015	0.072			
	75	8	1.170	0.080			
20	114	8	1.171	0.067			
	18	7	1.224	0.075			

ml at day 15 followed by a rapid rise to 1.292 gm/ml at day 18 was noted.

From figure 1 the mean weight of the fetus was observed to increase gradually till it equalled the combined weights of the placenta and the fluid on the 13th day. By the 15th day

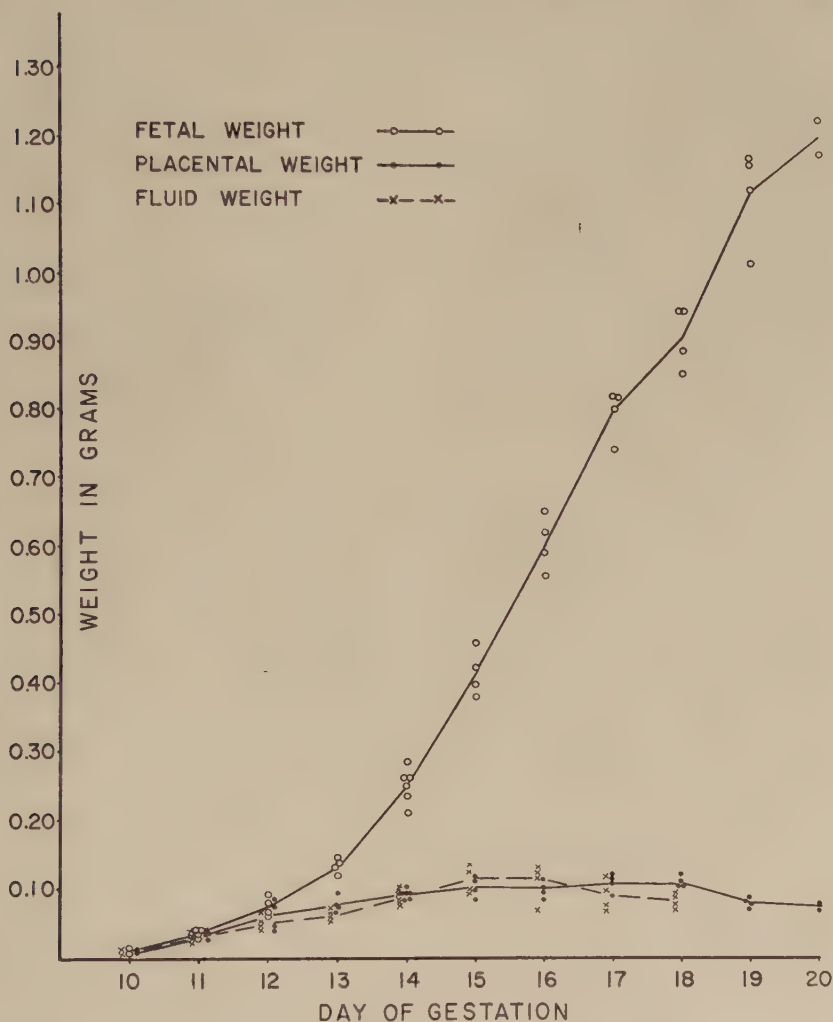


Fig. 1 The daily weight in grams of the fetus, the accompanying placenta, and the amniotic fluid in the final half of gestation. Each locus represents the average weight for one litter.

the fetal weight would probably have been greater than that of placenta, fluid, and membranes if the latter were included. On this day of gestation the amniotic fluid reached its greatest weight and then declined rapidly. From the 17th to the 18th day of development, there was apparently a slight governing of the growth rate and the entire graphic curve revealed a shallow sigmoid tendency.

In figure 2 the scale has been increased to show fluid volume trends more clearly. A projection of this curve in the initial stages of gestation pointed to the 9th day as the probable starting time of the initiated amniotic fluid production and there was a rise in volume from 0.01 ml on the 10th day to a peak of 0.12 ml on the 15th day. This was followed by a substantial decrease in fluid volume to .06 ml on the 18th day beyond which recording was not possible. Actually there was very little of the stringy fluid remaining at the time of birth. The greatest distribution of volumes occurred on the 16th and 17th days.

DISCUSSION

The observations reported here might be more easily interpreted if an examination of factors in the pattern of fetal mouse development were first considered. After the 8th day of development, there would be structural changes occurring, not so much in the embryo as in the decidual membranes and the placental structures.

As was noted by MacDowell, Allen, MacDowell ('27) and also by Enzmann ('35), the growth rate of embryos of different strains was slight during the 7 days preceding implantation, i.e., the manner of growth before the beginning of the embryo proper on the 7th day was different from that after this time. Their opinion was that the weight and age of the mouse from the 8th through the 18th day could be plotted arithmetically as a sigmoid curve. Figure 1 showed that the curve for fetal growth was slightly sigmoid with only one inflection point at the 17th day (stage) of gestation. Both of the previously mentioned investigations re-

vealed an inflection point on the 16th day using different strains of mice. Both stated also that the extra-embryonic structures were heavier in weight than the embryo itself until the 15th day. This would possibly be similar to the

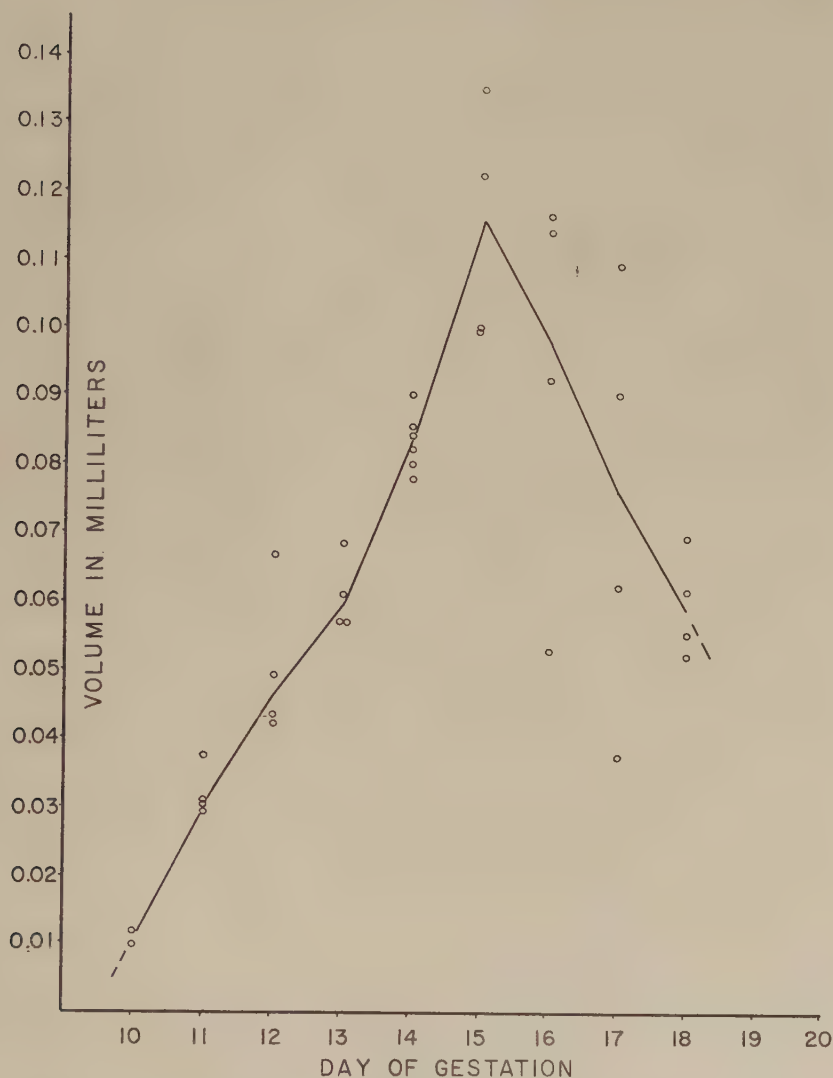


Fig. 2 The daily volume in milliliters of the amniotic fluid per fetus in the final half of gestation. Each locus represents the average volume for one litter.

weight curve in figure 1 if the decidual membranes had been included in the weighing.

Brooksby and Newton ('38) have shown that the placenta while intact and functioning retained water in the maternal body and also in the fetus, if the fetus were healthy and growing. Removal of the placenta from the uterine epithelium caused a reduction in maternal and fetal weight perhaps from a water release in the manner of an excretion.

Wislocki et al. ('46) and Bridgman ('48) have demonstrated in the mouse and rat, respectively, that the histology of the placenta proved deterioration at about the 17th day of gestation, which might explain the change in fetal and placental growth rate following the 17th day. On the other hand, it should be pointed out that Ibsen ('28) has warned that the placenta with its changing capacity for blood might show misleading measurements for the weight of placenta alone.

When comparisons of relative volume changes were made on the mammals for which amniotic fluid volumes were recorded, the graphical pattern of the mouse amniotic fluid more closely resembled those of the guinea-pig and hamster in the initial stages of development. But in most of the volumes studied a graphical change was evident generally in the final quarter of gestation. There appeared to be 4 groups into which the volume patterns could be placed. First, that group including the cat and guinea-pig which had a slight volume decline, followed by another climb until birth; second, the volumes of sheep and man which remained either stationary or declined slightly; next, those volumes of the sow and cow which showed a moderate to rapid decline; and finally the hamster, and particularly the rabbit, both of which presented very rapid declines until little fluid remained at parturition. The mouse apparently resembled the rabbit in the last grouping because of its rapid decline and the dirth of fluid on the final day of prenatal development.

SUMMARY

1. Observations on 42 litters of mice of the "BAF" strain were made to establish the relation of amniotic fluid weight to both fetal and placental weights at daily stages of gestation. The volume of amniotic fluid was recorded simultaneously.

2. The period of recorded gestation extended from the 10th to the 20th day. However, increased viscosity restricted measurement of the fluid after the 18th day. Parturition occurred generally on the 20th day.

3. Fetal weight gained gradually through the 13th day and then rose more rapidly to produce a shallow sigmoid curve. Amniotic fluid weight and placental weight increased slowly until the 15th and 18th day, respectively, and finally diminished. The fluid volume, closely resembling the fluid weight curve, increased to a maximum of 0.12 ml on the 15th day followed by a lowering to 0.06 ml on the 18th day of gestation. The specific gravity of the fluid was calculated and seen to decline generally to 1.020 on the 15th day, and to increase gradually to 1.292 on the 18th day.

4. The relative volume pattern of the mouse amniotic fluid more closely resembled those of the guinea-pig and hamster in the initial stages; those of the rabbit and hamster in the concluding phase of intrauterine development.

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PROCEEDINGS OF
THE FIFTY-SECOND ANNUAL MEETING OF THE
AMERICAN SOCIETY OF ZOOLOGISTS

MICHIGAN STATE UNIVERSITY
EAST LANSING, MICHIGAN

SEPTEMBER 6, 7, 8, 1955

The fifty-second Annual Meeting of the American Society of Zoologists was held at East Lansing in association with other societies of the American Institute of Biological Sciences. The beautiful campus, the excellent facilities for meetings and for the comfort of the visitors, the careful arrangements made by the local committee and the ideal weather all contributed to making the meetings memorable. Scientific sessions were well attended, discussion was brisk and profitable.

The business meeting was well attended, and the activities started under the leadership of President Viktor Hamburger were well received, their continuation ensured. This is discussed further in section 6. The excellent annual dinner was well attended, and the diners were addressed by Dr. Hamburger who gave to many members a new perspective on "organizers." The special sections arranged respectively by Drs. Ernst W. Caspari, Samuel Matthews, A. Glenn Richards and J. Paul Scott contributed markedly to the success of the meetings. These sections brought together papers which otherwise would have been scattered through the program, and added others which otherwise might not have been given. The two symposia were excellent, "Problems of Morpho-

genesis'' arranged by Dr. Hamburger, and ''Protozoa and Molecular Physiology'' arranged jointly with the American Society of Protozoologists by Dr. Paul Weisz. Unfortunately the latter was attended more extensively by members of the other society, the zoologists being drawn off to a great extent by the conflicting symposium presented by the Naturalists on ''Modern Approaches to Differentiation.'' This points up one of the difficulties inherent in meetings with the A.I.B.S. or the A.A.A.S.

Another real difficulty was illustrated by these meetings. In general the number of papers was smaller than the Society is accustomed to having. There were a number of reasons for this: (1) this meeting followed one at Christmas time, with therefore less than the usual period between meetings; (2) by using the September date we came into direct conflict with the meetings of the American Society of Physiology and the Society of General Physiologists, at Boston and Woods Hole. This led to a sharp shrinkage in the number of papers submitted in these fields; and these areas have constituted a large part of the meetings over a period of years. (3) When the Society meets with the AIBS it is necessary to set the deadline for papers nearly a month earlier than would be necessary for a separate meeting. This is due to the necessity of fitting our program into that of the entire group. The last two factors will tend to be continuing problems whenever we meet in the fall with the A.I.B.S.; and since the majority of our members seem to prefer meetings at this time (see section 8E) this problem will recur time and again. Members with ideas for overcoming these difficulties are urged to communicate with the officers of the Society.

THE BUSINESS MEETING

The meeting was called to order by President Viktor Hamburger with 78 members present.

1. Memorial resolutions.

GEORGE HOWARD PARKER

1864-1955

With the death of Professor George Howard Parker biological science lost one of its prominent leaders and the American Society of Zoologists one of its distinguished members. He was born in Philadelphia on December 23, 1864, and died, after a long illness, on March 26, 1955.

As a boy Parker attended Friends' Central School and showed an early interest in natural history that found expression in the collecting of minerals, insects and marine animals. An understanding father introduced him to the Philadelphia Academy of Natural Sciences which had substantial influence on Parker's early scientific education. The financial panic of 1877 brought difficulties that necessitated his leaving school to help support the family. In 1880 he was appointed a beneficiary of the Philadelphia Academy, which, for a term of two years, permitted him to work with a congenial group in natural history. This experience aided in turning him from the undisciplined acquisition of specimens and adolescent adventures in the violent aspects of elementary chemistry to a more formal and directed interest in science. In 1883 he entered Harvard College, from which he received the B.S. degree in Natural History in 1887, and, continuing into graduate study, the D.Sc. degree in 1891. His doctoral dissertation was on the structure of compound eyes in crustaceans.

Award of a travelling fellowship enabled Parker to spend the following two years in the laboratories of several German universities, and at the Stazione Zoologica in Naples. The beautiful country-side around the Gulf of Naples, the pleasant leisurely life of this region, and the stimulation coming from an international group of investigators invariably in attendance at the Stazione, made Parker a strong Italianophile.

On his return to Cambridge, Parker resumed his duties as instructor in the zoology department at Harvard University. Promotion to the professorship came in 1906, and in 1921 he was appointed Director of the Zoology Laboratory, a post he held until his retirement from active teaching in 1935.

Distinctions and honors came readily to Parker. He was a member of the National Academy, of the American Philosophical Society, a trustee of the Marine Biological Laboratory at Woods Hole, president of the Society of Naturalists, of the Society of Zoologists, of the American Academy of Arts and Science, and of Sigma Xi. He was elected to honorary membership in a number of foreign academies and state academies in this country.

In outward appearance Parker was a man of almost austere, imposing dignity, but this impression soon vanished on closer acquaintanceship. His colleagues at Harvard, and those at Woods Hole, knew him as a friendly amiable person, showing flashes of puckish humor, and as a raconteur of anecdotes about the older biologists of his young days. To many of the graduate students at Harvard this facet of Parker gleamed at the daily departmental teas; with growing acquaintanceship came invitations to the student to share in Sunday walks; these consisted

of a good jaunt over some of the suburban Boston country-side, and were invariably capped by dinner at one of a large number of foreign restaurants at which Parker was a favored patron.

Parker's early research interests were on the structure and function of the nervous system in lower animals, an interest which persisted throughout his lifetime and actually constituted the major portion of his scientific work. His studies on the elementary nervous system and the physiology of sense organs were recognized as classics in their field.

Later in his career Parker turned to a closer investigation of the control of effectors, using the chromatophores of fishes, amphibians and reptiles for his experimental material. The early investigators of color changes in animals believed that this function was predominantly under the direct control of nerves, but studies in the first and second decades of this century demonstrated the participation of a humoral agent in this regulation. Parker proceeded to develop the view that while the initial step in the activation of chromatophores as effectors was a nervous stimulation acting through the eyes, impulses passed from these photoreceptors either to endocrine glands whose secretions were transported through the blood to the chromatophores, or over nerve fibers to terminals from which secreted substances diffused into the chromatophores in the immediate vicinity of these nerve terminals; in this way the distinction between the two types of activation was minimized, and brought into line with the concept of chemical mediators in nervous activity.

Parker's best known characteristic as a scientist was the directness and simplicity of his experimental approach to a problem. In an age where instrumentation was becoming increasingly important in biological research Parker's apparatus rarely consisted of anything more than ordinary laboratory glassware. Despite this directness of approach, Parker was not without appreciation and respect for technical skill in experimental work. In his early studies of color changes in elasmobranch fishes, it became necessary to hypophysectomize animals; in what might be called a Parkerian approach, he cut away the lower jaw to give free access to the roof of the pharynx from which an opening could be made in the floor of the skull to remove the pituitary gland. Parker was troubled, however, that the animals did not long survive such surgery. When one of his former students did some really skillful hypophysectomies for him, avoiding the traumatization that followed from Parker's surgery, and the animals survived for several weeks, Parker's delight and admiration knew no bounds.

Another outstanding feature of Parker's scientific character was the striking absence of personal feelings or animosities. He was raised in a scientific tradition in which polemical controversy was not uncommon, yet none of this appears in Parker's publications. He could differ with other investigators, as they sometimes did with him, but rather than resenting such differences of opinion or interpretation as a personal attack, he held that "we must declare our find and submit it to others for test". . . we are by our very nature driven to seek the confirmation of those who travel the same road with us."

L. H. KLEINHOLZ

CHARLES FREEMAN WILLIAMS McCLURE

With the death of Professor Charles Freeman Williams McClure the American Society of Zoologists lost one of its oldest and most distinguished members. He was born in Cambridge, Massachusetts, March 6, 1865 and died in Princeton, New Jersey, July 23, 1955. He was one of the early members of the American Morphological Society which was a progenitor of the American Society of Zoologists. His association with these two societies covered a period of well over a half century.

Professor McClure's early education was in private schools in Cambridge and Boston and at Phillips Exeter Academy. He received the A.B. degree from Princeton University in 1888. During the next two years he remained at Princeton as Fellow in Biology, working especially under Professor Henry Fairfield Osborn. He then continued his studies at the College of Physicians and Surgeons in New York. As his interests turned more and more to comparative morphology he went abroad to study at Berlin, Kiel and Würzburg. He received the A.M. degree from Princeton in 1892 and the honorary degree of Sc.D. from Columbia University in 1908.

Professor McClure became a member of the Princeton Faculty in 1891 and remained at Princeton for the remainder of his life. He was appointed Professor of Zoology in 1905, and was made the first incumbent of the Class of 1877 Chair of Zoology in 1909. He became Professor Emeritus in 1935.

Early research interests of Dr. McClure were in the embryology of the nervous system, particularly the primitive segmentation of the vertebrate brain and he carried on notable work in this area. Soon, however, he turned his attention to the development of vascular structures and research on this subject occupied him during most of his life. In the period between 1900 and 1930 he published over 30 papers which dealt either with the blood-vascular or the lymphatic system of vertebrates. In much of this work he had the collaboration of his close friend and colleague, Dr. George S. Huntingdon of the College of Physicians and Surgeons, Columbia University.

His work on vascular structures centered around two main problems: the developmental anatomy of the great veins, particularly the posterior vena cava; and the origin of vascular endothelium. Dr. McClure was long recognized as a leading authority on the development of the vertebrate venous system and the embryological interpretation of venous anomalies. His monograph, "The Mammalian Vena Cava Posterior," summing up much of his work, stands as a classic in the field.

For a number of years the problem of the embryonic origin of vascular endothelium represented one of the most active fields of research in vertebrate embryology and led to what came to be known in the decade between 1910 and 1920 as the "endothelial controversy." Dr. McClure became concerned especially with the manner in which lymphatic endothelium and early lymph channels arise. His research ranged from a study of the normal development of thoracic ducts and jugular lymph sacs in mammals to experimental studies on lymphatics in fishes and amphibians. He became convinced of the local origin of endothelium from embryonic mesenchyme, which was in opposition to the angioblast theory of His

and the corollary concept that lymphatic endothelium arose by budding from venous endothelium. He vigorously supported his point of view at scientific sessions and in published papers, presenting evidence from his beautiful and painstaking research.

In connection with his research and teaching Dr. McClure began early in his career to build up at Princeton a Museum of Comparative Anatomy. He secured specimens from a great variety of sources in this country and abroad and skillfully trained a preparator, C. F. Silvester, to assist him. The result was his great collection of dissections, corrosions and reconstructions illustrating the comparative morphology of vertebrates. It is doubtful whether the McClure collection is excelled by any other in this country.

Dr. McClure was an excellent example of teacher-scholar. Although he was always deeply concerned with some aspect of his research, he was at the same time equally interested in teaching and in his students. For over 40 years he taught the undergraduate and graduate courses in Comparative Anatomy and Vertebrate Embryology at Princeton. His stimulating lectures were always illustrated by a wealth of material from his great collection.

Professor McClure loved to travel. In his youth he spent a great deal of time in the west. He also traveled extensively in Europe and had a wide acquaintance among his contemporary European zoologists and anatomists. In 1899 he was a member of the Admiral Perry Relief Expedition which restocked the arctic explorer's Greenland bases.

In 1921 he married Grace Latimer Jones, formerly head of the Columbus School for Girls, who survives him. Their home in Princeton, "Charmingfare," was a place where undergraduate and graduate students liked to assemble and where Dr. McClure loved to recount interesting episodes from his years of research and travel.

ELMER G. BUTLER

2. *Minutes.* The minutes of the 1954 meeting, as circulated in the form of Proceedings, were unanimously approved.

3. *Treasurer's report.* The report of the Treasurer, Theodore Jahn, approved by an auditing committee consisting of Ross Nigrelli and A. Glenn Richards, was accepted unanimously and is given below:

DECEMBER 23, 1954 - SEPTEMBER 1, 1955

Credits:

Cash balance from 1954	\$4,210.37	
Receipts from dues	3,872.00	
U. S. Savings Bond M16486998F	740.00	\$8,822.37

Debits:

Secretary:

Rudolf Kempton (Misc.)	\$199.96	
Secretarial assistance	426.55	626.51

Treasurer:

D. P. Costello — Chapel Hill	500.00	
Secretarial assistance	160.00	
Stamps	48.00	
Bank charges	1.27	709.27

Wistar Institute:

Addressing envelopes	14.18	
Reprints, abstracts, etc.	1,123.74	
Questionnaire, announcements	197.62	
New plates, printing, etc.	189.54	
Printing, postage, etc.	228.13	1,753.21

American Institute of Biological Sciences	818.00	
Biological Abstracts	971.00	
Bank Balance of September 1, 1955	3,204.38	
U. S. Savings Bond M16486998F	740.00	

\$8,822.37

4. *New Members.* Dr. Hamburger reported the action of the Executive Committee in promoting Associate Members to Members, and in electing new Members and Associate Member. The actions were as follows:

ASSOCIATE MEMBERS PROMOTED TO MEMBERS

Samuel Bieber, Wellcome Research Laboratories	David M. Morris, North Texas State College
Richard A. Edgren, G. D. Searle and Company	Paul F. Nace, New York Medical College
James Forbes, Fordham University	Wilbur S. Newcomer, Oklahoma A. and M. College
Richard J. Goss, Brown University	Edwin J. Robinson, Jr., Kenyon College
James H. Gregg, University of Florida	F. M. Sturtevant, G. B. Searle and Company
Ernest L. Hunt, Emory University	Charles M. Vaughn, University of South Dakota
Perry M. Johnston, University of Arkansas	Frank N. Young, Jr., Indiana University
Robert C. King, Brookhaven National Laboratory	
Aaron J. Ladman, Harvard University	
Clement L. Markert, University of Michigan	

NEW MEMBERS

- Robert D. Allen, University of Michigan
Norman G. Anderson, Oak Ridge National Laboratory
Lucena J. Barth, Columbia University
Marion A. Brooks, University of Minnesota
John H. D. Bryan, Iowa State College
Jack W. Daugherty, Rice Institute
William R. Dawson, University of Michigan
Melvin J. Fregly, Harvard University
Joseph F. Gennaro, Jr., State University of New York
Frederic A. Giere, Luther College
Stanley R. Glasser, University of Rochester
Margaret C. Green, National Science Foundation
John R. Gregg, Columbia University
Jean A. Gross, University of California at Los Angeles
Paul R. Gross, New York University
Clifford V. Harding, Jr., Wistar Institute
Bronislaw M. Honigberg, University of Massachusetts
Jack C. Jones, National Institutes of Health
Betty C. Moore, Columbia University
Jane H. Overton, University of Chicago
Helen A. Padykula, Harvard University
Mohammed T. M. Rizki, Yale University
Paul F. Robinson, Army Medical Center
Paul S. Stokely, University of Notre Dame
Alexander A. Wolsky, Fordham University

ASSOCIATE MEMBERS

- John M. Allen, University of Michigan
Everett Anderson, State University of Iowa
Adam Anthony, Pennsylvania State University
Thomas S. Argyris, Harvard University
Mary C. Barsa, Fordham University
Roger H. Bowman, Bucknell University
Chih Ye Chang, State University of Iowa
Walter Chavin, Wayne University
John A. Davison, Washington University
Clarence F. Dineen, University of Notre Dame
William G. Erwin, Northwestern State College
Frank J. Etges, University of Cincinnati
Frank J. Finamore, University of Illinois
Werner G. Heim, University of California at Los Angeles
Walter J. Kenworthy, Brown University
William B. Kinter, Harvard University
Ethel Sue Lumb, Vassar College
David J. McCallion, University of Toronto
Harold W. Manner, Syracuse University
Robert W. Merriam, University of Pennsylvania
Charles Norman, West Virginia University
Kenneth Ottis, Alabama Polytechnic Institute
Joy B. Phillips, Drew University
Charles L. Ralph, Northwestern University
Laurens N. Ruben, Princeton University
Robert S. Schmidt, Illinois State Normal University

Joseph L. Scott, University of Connecticut	Kenyon S. Tweedell, University of Maine
Leroy C. Stevens, Jr., Jackson Memorial Laboratory	Ronald A. Ward, Chicago Natural History Museum
Margaret C. Tavalga, American Mu- seum of Natural History	Stanley Weinreb, University of Wisconsin
	Jacob E. Wiebers, Purdue University
Promotion to Membership	17
New Members	25
New Associate Members	33

5. *Constitutional Amendment.* The amendment providing for a three-year term as President-elect, President and Past-president, one year in each category, and thus placing all officers and members of the Executive Committee on three-year terms, was voted unanimously by those present. Including the mail ballot, this brought the vote on the question to 379-2, thus producing more than the required 2/3 majority of those voting.

6. *The "Policy Committee."* President Hamburger discussed briefly his appointment of a temporary "Policy Committee," speaking essentially as follows:

In recent years, a number of members expressed concern over the performance and policies of the ASZ, and some pessimists felt that the Society has lost some of its appeal and vigor and that altogether the time would approach when there would be no longer an ecological niche for the subspecies "Zoologist" on the biological scene. It is true that the ASZ, like other societies of similar venerable age, suffers from the repercussions of the irreversible process of specialization and progressive differentiation, familiar to embryologists, which is going on in all fields of science. A number of Societies in specialized fields have split off and started a vigorous life of their own, such as Geneticists, Microbiologists, Ecologists etc. Their activities and meetings have taken over some of the functions which the ASZ used to fulfill, and this resulted inevitably in a conflict of loyalties of the members.

When I took office I found that the situation in the ASZ is far from gloomy. Many valuable and constructive suggestions for improvements and for the strengthening of the Society had been submitted; and when I talked these matters over with some older and younger members, I was greatly encouraged by their genuine interest in the affairs of the Society, by their constructive, forward-looking attitude and their willingness to cooperate in an effort to improve the situation. I am convinced that the Society, far from being moribund, can draw on strong resources for leadership and loyalty.

For years, criticism has centered around the choice of *time and place of meetings*. This problem is an eternal headache for the Executive Committee. Following suggestions by some members, the questionnaire was sent out which you are familiar with. We did not expect clear-cut directives, but the answers from about 25% of the members showed some definite trends of thinking and the Executive Committee has obtained some valuable guidance for its policy. Our Secretary, Dr. Kempton, has done an excellent job in evaluating the data. These and his pertinent conclusions have been placed in your hands. (Note: see summary in section 8E.)

The second step I undertook was the *appointment of a temporary Policy Committee*, early this summer. This Committee was asked to do some thorough soul-searching, to deliberate some specific changes and improvements that had been suggested and others that might be brought up by its members and if possible to submit a preliminary report at the present meeting. Dr. John Buck accepted the Chairmanship; other members were Drs. Ladd Prosser, Clifford Grobstein and Edgar Zwilling. They were chosen deliberately from the Woods Hole contingent of the membership to facilitate the meeting of the group. Dr. Buck held an open meeting at Woods Hole, which was attended by 15 other people interested in the Society, in addition to the Committee. According to eye-witnesses, the discussions were very spirited and fruitful, and some real progress was made at that meeting. Dr. Buck has drafted a report of these deliberations which he will submit presently. I want to take this opportunity to thank Dr. Buck for his effective leadership and generous sacrifice of time and energy. It is due to his efforts that concrete and substantial proposals can be submitted to you already at this early date.

Dr. John Buck then presented to the meeting the following report from the temporary Policy Committee:

As indicated by President Hamburger, the Policy Committee is not a new departure but a formalizing of previous efforts at improvement of the Society. In this connection the Committee was fortunate to be able to refer to numerous letters from interested members, to the Schrader report on program-improvement, to the Jahn recommendation on the basis of membership, to the Browman analysis of membership geographical distribution, and to the Goodrich report on the composition of the Executive Committee. The last has led already to the constitutional amendments approved during the last two years which enlarged the Executive Committee and placed all its members and all officers on three year terms.

The Policy Committee started work with no specific objectives in mind other than to sift membership opinion in search of suggested changes for which there was strong support, but did consider the following general problems as falling within its province: (1) Improve-

ment of the Society as a society — such as administrative efficiency, membership *esprit de corps*, etc. (2) Measures bettering present society activities — such as program improvement. (3) Measures affecting the Society's mission — such as efforts to strengthen zoology as a profession, improve the teaching of zoology etc.

Besides holding the pilot meeting mentioned by Dr. Hamburger and analyzing the letters from members, the Committee proceeded along the following lines:

(1) It circulated a fairly extensive questionnaire to all members known to have ever expressed a written opinion about the Society, *pro or con* (total of about 40).

(2) It studied a survey of the programs at the annual meetings for the years 1939–1954 to look for trends in number and type of papers presented and abstracts submitted. (Data kindly assembled by Dr. M. L. Keister.)

(3) It studied the tabulation (given below) of overlapping membership of ASZ members in 19 other zoological societies to assess membership loyalties and overlap of fields. (Data on 15 societies supplied by the A.I.B.S., the rest by Dr. Keister.) In the time available it was not possible to find data for the American Society of Mammalogists or recheck the A.I.B.S. figure for the Society for the Study of Evolution.

	APPROX. TOTAL MEMBERS ¹	% OF MEMBERS ALSO IN ASZ ¹	% ASZ MEMBERSHIP JOINT ¹
Nat. Assoc. Biol. Teach.	1660	1.4	1.8
Amer. Soc. Parasitol.	805	10	6.5
Soc. Gen. Physiol.	250	40	7.5
Am. Genetics Assoc.	1200	4	3.8
Am. Soc. Limnol. and Oceanog.	1100	9	8
Am. Soc. Human Genetics	565	11	4.5
Assoc. Southeast. Biol.	535	10	4
Ecol. Soc. of Amer.	1250	9	8
Soc. Study Develop. and Growth ²	270	50	10.5
Amer. Soc. Ichthyol. and Herpetol.	1200	6	5
Amer. Soc. Anat.	935	23	20
Amer. Physiol. Soc.	1425	12	13
Amer. Soc. Natural. ²	470	40	15
Genetics Soc. Amer.	980	16	12.6
Soc. Study Evolution	860	0.2	0.15
Soc. Systemat. Zool.	1300	11	11
Entomol. Soc. Amer.	1025	6.5	5
Amer. Soc. Protozool.	515	19	8
Amer. Microsc. Soc.	555	27	11
No other A.I.B.S. Society			32

¹ Comparisons between societies are mostly based on 1952 figures, the latest available from the A.I.B.S., but total membership is given for a later year in some cases.

² Not a paper-reading society.

Among the findings of the Committee are the following :

(1) Over the past 15 years, during which there seems to have been no significant change in emphasis, the principal fields represented in the programs of the national meetings of our Society have been physiology (30%), embryology — developmental endocrinology (37%) and cytology (10%). No other field has averaged more than 4% and several are much lower.

(2) In the past 15 years our membership has increased 45%, but the total number of papers in the annual program decreased 13%.

(3) We have held our own in physiology in spite of the founding, in 1946, of the small but active Society of General Physiologists. However, in view of the fact that the number of physiologists has doubled since 1940, a relative decline in program content may actually have occurred. (The same may be true in other fields but no data were available.)

(4) About 430 of our 1300 members belong to no other A.I.B.S.-associated society.

It appears, in sum, that there is no immediate cause for alarm over the Society; the meetings are well attended and membership is growing. On the other hand it is clear that our programs are seriously out of balance due to the fact that we have almost completely lost the participation of members in a number of important subdivisions of Zoology.

Recommendations. Society opinion on many important matters — program content and improvement, zoological education, abstracts, regional meetings, etc. — was too varied to enable the committee to formulate any recommendation during the short summer period available, but the following items, which appeared to be strongly favored in the opinions sampled, were judged ready to recommend to the full membership :

- (1) Abolition of the present two classes of membership.
- (2) Nomination of two candidates for each vacant officership and Executive Committeemanship.
- (3) Elections by mail ballot.
- (4) The creation of a new office, that of Program Secretary, to relieve the Secretary of the responsibility for the arrangement and publication of the programs for the annual meeting.

CLIFFORD GROBSTEIN
C. LADD PROSSER
EDGAR ZWILLING
JOHN BUCK (Chairman)

Dr. Hamburger then addressed the meeting again, making the following points:

As Dr. Buck has indicated, several points require constitutional amendment; some points have been sufficiently clarified by the Policy Committee; others require further consideration. The Executive Committee has not taken a stand on any of the proposals; it wishes the membership to express its view and to vote on the proposals without prejudice. In line with this the Executive Committee has voted:

- (1) To circulate a questionnaire on the matter of *change of membership classes*. This will be a poll of opinion and not a final vote, and is designed to give information which will permit the formulation of a proposed constitutional amendment which can be answered by a "yes" or "no" vote. Such a proposed amendment will be submitted to the membership later in the year, together with others mentioned below, with a summary of arguments for and against the amendment.
- (2) To submit to the membership amendments which would (1) ensure the nomination of two candidates for each opening among the Officers and the Executive Committee, and (2) would provide for voting to be carried on by mail instead of at the annual meeting.
- (3) To submit to the membership an amendment proposing the creation of the office of Program Secretary.
- (4) To request this meeting to authorize the formation of a new Policy Committee, again under the Chairmanship of Dr. John Buck, to continue and complete the work of the first provisional Committee, and to report at the next meeting. The membership of this Committee would be more representative geographically and with respect to special fields of Zoology than was the first.

I hope you have gotten the impression that things are moving in the right direction and that an optimistic spirit prevails. However, I should like to point out that in the final analysis the revitalization can be successful only if the membership at large takes an active interest in the affairs of its Society. The Executive Committee and the Policy Committee invite you to submit your criticisms and suggestions, and we assure you that they will be given serious consideration and that the membership will be kept informed of all further steps. If any trends can be detected in these first steps, it is toward a more active participation of the membership and toward the service to the interests of *all members*, including those who are primarily engaged in teaching and administration.

After some questions and discussion, including much favorable comment, it was VOTED to authorize the appointment of a new Policy Committee, under the Chairmanship of Dr. John Buck, to proceed with a study of the Society and its problems, and to authorize the use of Society funds for the purposes of the Committee.

7. *Election of Officers.* Following the report of Dr. Hope Hibbard for the Nominating Committee consisting of herself, Edgar Zwilling and Donald Costello, Chairman, the slate of officers was elected unanimously. It will be noted that certain nominations were made in addition to those circularized in the spring, a necessity caused by resignations.

President: Tracy M. Sonneborn (one year).

Vice-President: John B. Buck (one year).

Executive Committee: Viktor Hamburger (one year); Elmer G. Butler (three years); Douglas A. Marsland (three years).

Representative of the Society on the Board of Governors of the American Institute of Biological Sciences: John B. Buck (four years).

Representative of the Society on the Advisory Editorial Committee of Biological Abstracts: Eleanor Slifer (four years).

Representative of the Society on the Executive Committee of the Biological Stain Commission: Frank H. J. Figge (one year).

Representative of the Society on the Board of Trustees of the American Type Culture Collection: R. P. Hall (one year).

Members of the Editorial Board of the Journal of Morphology: (three years): Jane Oppenheimer, Ernst Scharrer, Paul B. Weisz.

8. *Other actions by the Executive Committee.* Dr. Hamburger reported to the meeting the following additional actions of the Executive Committee.

A. Election of Dr. Clarence L. Turner as Life Member.

B. Ratification of the new constitution of the American Institute of Biological Sciences. The main practical effect this action has upon the Society is to increase from about \$800 to \$1,000 the amount the Society pays the AIBS for dues of its members.

C. Appropriation of \$200 for the expenses of the Policy Committee, to be available if the meeting continued this committee.

D. In view of the reduction of our cash balance during the past year, the increased assessment paid to A.I.B.S., the possible expense of the Policy Committee, it was voted to return dues to the level stated in the constitution, namely \$5.00. During 1953-55 the dues had been reduced to \$4.00.

E. Policy in relation to selection of places of meeting. While it was recognized that one Executive Committee cannot legally bind the action of future committees, the Executive Committee voted the following policy which it felt should be followed at least until such time as the Policy Committee is ready to make further recommendations:

(1) As a basic consideration it should be known that the results of the questionnaire on time and place of meeting gave the following approximate results:

- (a) About two out of three of our members consider the time of meeting more important than the place.
- (b) Of each 4 members, two prefer to meet in September, one prefers December, one prefers to alternate the two times.
- (c) Of each 5 members, two prefer to meet with the A.I.B.S., one prefers to meet with the A.A.A.S., two prefer to alternate meetings with these organizations with separate meetings or to always meet alone (the last a small fraction).

(2) As a matter of policy the best way for the present to meet these desires of the majority without damaging the interests of the minority, would be to follow these principles:

- (a) The Society should meet about twice as frequently with the A.I.B.S. as with the A.A.A.S.
- (b) In years in which the Society meets with the A.I.B.S. we should also participate in the A.A.A.S. meeting at least to the extent of sponsoring Symposia.

- (c) As opportunity presents itself occasional separate meetings should be held in approximately the proportion of one year in four.
- (d) An attempt should be made to so arrange meetings that their frequency in geographical areas will be in rough proportion to the number of members residing in those areas.

F. In view of the fact that except for the solo meeting at Chapel Hill our immediately preceding meeting was with the A.A.A.S., and in view of the expressed preference for fall meetings, it was voted that the next meeting would be held with the A.I.B.S. at the University of Connecticut at Storrs, August 27-30, 1956. (The voting by members on the specific issue of AIBS at Storrs or AAAS at New York was inconclusive — 54% desiring Storrs, 46% preferring New York.)

9. DR. JOHN A. MOORE, our Representative in the Division of Biology and Agriculture of the National Research Council, made the following report.

This year's Annual Meeting of the National Academy of Sciences — National Research Council Division of Biology and Agriculture was held in Washington on May 13th and May 14th.

Dr. Paul Weiss as Chairman gave an interesting and detailed report on the activities of the Division of Biology and Agriculture for the past year. The following activities and plans for activities are of special interest to the American Society of Zoologists.

The Biology Council has formed a number of "Task Forces" to deal with specific problems which are judged to merit action. "Task Forces" are now dealing with

- (1) Public Relations
- (2) The Conceptual Framework of Biology
- (3) Research Structure and Support
- (4) Biological Materials, and
- (5) Techniques and Technician Training.

The reports of these "Task Forces" can be awaited with interest.

The Biology Council has a committee on Education Policies which is surveying the questions of Pre-college Education, Teacher Recruitment and Education, College Education, Graduate and Professional Education, Biology in the Medical Sciences, Applied Biology, Publications, and Adult Education.

One of the most important activities of the N.A.C.-N.R.C. is its responsibility in the screening of fellowship applications, principally for the National Science Foundation. The screening committees do not make awards, they merely recommend. There were 635 applications for N.S.F. graduate fellowships in biology and 167 awards were made. There were 207 applications for N.S.F. post-doctoral fellowships in the biological and medical sciences and 19 awards were made.

Dr. Paul Weiss, with this meeting, completed his term as Chairman. He is succeeded by Dr. L. A. Maynard, who has served in recent years as Vice-chairman. The new Vice-chairman will be Dr. P. C. Mangelsdorf.

10. DR. HAROLD H. PLOUGH, our Representative on the Council of the American Association for the Advancement of Science, made the following report.

The 1954 meeting of the AAAS was held in Berkeley, California on the campus of the University of California, December 26-31, 1954. The major program for contributed papers in the biological science was run by the Western Society of Naturalists but extensive programs were given by the Society of Systematic Zoology, the Society of Ichthyologists and Herpetologists, and the Ecological Society. An excellent series of symposia were held which cut across a number of fields. Those which aroused the greatest interest were: the program of the International Conference on Animal Venoms, and the two sessions on "The Cell." Genetics was not represented in the program.

At the two Council meetings, the item of major interest was the discussion of a motion made by your representative that the AAAS appoint a committee to consider and report on the hazards of radiation to human populations from the nuclear detonations at Nevada and the Pacific Islands. It was voted to authorize the president to appoint such a committee to report at some future time. At a later meeting of the council during the year, it was announced that the National Academy of Sciences had already authorized such a study with financial support from the Rockefeller Foundation and, therefore, the appointment of the AAAS committee was temporarily postponed.

In June 1955, your representative received several letters from members protesting against the holding of the meeting of the AAAS in Atlanta in 1955 because of the continued policy of the State of Georgia in segregation of non-white citizens. It was suggested that Negro members of the Society would be subjected to discrimination at the meeting. Your representative wrote a letter of protest against the holding of the meeting in Atlanta and requested reconsideration and a shift in the place. This was considered with other protests at a

meeting of the Executive Committee on June 12, 1954 and the enclosed memo adopted and published in *Science* on June 24th. It was believed unwise to discriminate against Southern cities in spite of the continued segregation policy. It was felt that a meeting would recognize slow progress in removal of segregation barriers, and that the protests engendered might actually be of greater aid in the more rapid removal of the barriers than would be the policy of ignoring them by meeting elsewhere. Negro members will be free to attend all meetings but will be discriminated against only by being refused rooms at certain hotels.

Finally your representative wishes to emphasize that it is important for the Society to meet with the AAAS occasionally. It seems especially desirable that a joint meeting be held along with AAAS in New York in 1956. The following year, 1957, the meeting will be in Indianapolis and in 1958 in Washington, D. C.

The existence of a national organization of scientists like AAAS is important for every branch of science. Its importance will be considerably diminished unless member societies hold joint meetings of some sort with it occasionally.

11. DR. EMIL WITSCHI pointed out that in three years there will be another International Zoological Congress. It was moved and VOTED unanimously, that the President appoint a small committee to consider relations of the Society with Congresses, and especially with this one.

12. *Addresses wanted.* Mail to the following members has been returned to the sender. Anyone having information concerning the proper present address should notify the Secretary.

Allen, M. Joan	Evans, Llewellyn T.	Randall, Walter C.
Abbott, Cyril E.	Gayer, H. Kenneth	Riddle, Oscar
Blane, Richard	Hefley, Harold Martin	Rubin, Capt. David
Browning, Iben	Kendall, James	Smith, Harry M.
Chase, Col. Hyman Yates	Lund, Everett Eugene	Talbot, Mary
Denison, Mary Eileen	Potzger, Margaret	Young, R. T.
Dent, James N.	Pettibone, Marion	Zaletsky, Moses

13. DR. VICTOR HAMBURGER spoke feelingly of the debt of gratitude owed by the Society to Michigan State University, and especially to the members of the local committee: Drs. Karl Stiles, Donald W. Hayne and James C. Braddock. He paid tribute to the excellence of the arrangements, and commented on the burden carried by these biologists for the welfare of the meetings.

AMERICAN SOCIETY OF ZOOLOGISTS

CONSTITUTION

(As Amended by the Society at the Business Meeting, September 6, 1955.)

ARTICLE I

NAME AND OBJECT

Section 1. The Society shall be called the "American Society of Zoologists."

Sec. 2. The object of the Society shall be the association of workers in the field of zoology for the presentation and discussion of new or important facts and problems in that science and for the adoption of such measures as shall tend to the advancement of zoological science.

ARTICLE II

MEMBERSHIP

Section 1. The membership of the Society shall consist of two classes:

a. Associate membership open to all actively engaged in the field of zoology who have had training in zoology equivalent to that required for the doctorate degree.

b. Active membership open to those who hold the doctor's degree in zoology or who have done work equivalent thereto and who, in addition to the usual requirements for this degree, have published the results of substantial zoological research.

Sec. 2. Election to membership in the Society shall be upon recommendation of the Executive Committee.

Sec. 3. Associate members shall not hold office or vote, but may present papers before the Society without introduction. Associate members shall receive all literature issued by the Society, including the proceedings of the Society, and shall have the same privileges as active members in journal subscriptions.

Sec. 4. Associate members may be elected to active membership in the usual way when the research requirements of active membership have been met.

ARTICLE III

OFFICERS

Section 1. The officers of the Society shall be a President-Elect, a President, a Past-President, a Secretary and a Treasurer. The President-Elect shall be elected at one annual meeting and shall then successively and automatically become President and Past-President at the next two annual meetings. The Secretary and Treasurer shall be elected triennially and shall serve three years.*

* The term "year" wherever it appears in the Constitution and By-Laws refers to the variable period extending from the end of one annual meeting through the next annual meeting.

Sec. 2. The Executive Committee shall consist of the officers and six members elected from the Society at large. Of the six members at large, two shall be elected each year to serve three years. (Thus all members of the Executive Committee, both officers and members at large, shall serve three year terms.) If any member at large shall be elected to any office, resign, or otherwise become unable to serve on the committee, a member at large shall be elected at the next annual meeting of the Society to serve the remainder of his term. No member of the Executive Committee except those who have not served a full term shall be eligible to succeed himself until a year after his term expires.

Sec. 3. Election of officers and of members at large of the Executive Committee shall take place by ballot at the annual meeting of the Society, except as provided below (section 5). All terms of service shall commence with the close of the annual meeting at which the incumbent is elected.

Sec. 4. The officers named in Section 1 shall discharge the duties usually assigned to their respective offices. (See by-laws.)

Sec. 5. Vacancies in the board of officers, occurring from any cause, may be filled by election by ballot at any meeting of the Society. A vacancy in either the Secretaryship or the Treasurership occurring in the interval of the meetings of the Society may be filled, until the next annual meeting, by appointment by the Executive Committee.

Sec. 6. At the annual meeting the President shall name a nominating committee consisting of three active members. It shall be the duty of this committee to nominate officers of the Society, including the permanent representatives which the Society is asked to name to various boards and councils. This committee shall make its nomination to the Secretary at least four months before the next annual meeting. Additional nominations for any office may be made in writing to the Secretary by any five members at any time previous to balloting.

ARTICLE IV

MEETING OF THE SOCIETY

Section 1. Unless previously determined by the Society, the time and place of the annual meeting shall be determined by the Executive Committee. Special meetings may be called and arranged for by the Executive Committee. Notices of such meetings shall be mailed to all members of the Society at least two weeks before the date set for the meeting.

Sec. 2. Sections of the Society may be organized in any locality by not less than ten members, for the purpose of holding meetings for the presentation of scientific papers. Such sections shall have the right to elect their own officers and also associate members; provided, however, that associate membership in any section shall not confer membership in the Society.

ARTICLE V

QUORUM

Twenty-five members shall constitute a quorum of the Society and four a quorum of the Executive Committee.

ARTICLE VI

CHANGES IN THE CONSTITUTION

Amendments to this Constitution may be adopted at any meeting of the Society upon approval of two-thirds of the members voting, subject to the following conditions:

a. The proposed amendment must be in writing and signed by at least five members of the Society.

b. This signed proposal must be in the hands of the Secretary at least one month before the meeting of the Society at which it is to be considered.

c. The Secretary shall mail copies of the proposed amendment to the members of the Society at least two weeks before the meeting.

d. Members unable to attend may submit their votes in writing to the Secretary.

BY-LAWS

ARTICLE I

DUES

Section 1. The annual dues for active and associate members, unless remitted or changed by the vote of the Society, shall be five dollars.

Any member in good standing, having paid annual dues to the Society for not less than twenty-five years, who shall change his professional status, may apply to the Executive Committee for the remission of further dues. Applicants approved by the Executive Committee shall be exempt from further payment of dues, but such members shall be entitled to all the privileges of membership formerly enjoyed.

Sec. 2. Any member in arrears of dues for two years should be dropped by the Executive Committee. Upon payment of arrearage he shall be reinstated.

ARTICLE II

PRESIDENT

Section 1. The President shall preside at scientific sessions and at the business meetings.

Sec. 2. He shall also appoint the committees prescribed by the constitution and by-laws.

ARTICLE III

PRESIDENT-ELECT

Section 1. The President-elect shall preside at sessions designated by the President.

Sec. 2. He shall also assume the duties of the President in the latter's absence.

ARTICLE IV

SECRETARY

Section 1. The Secretary shall keep the records of the Society.

Sec. 2. He shall be responsible for all arrangements for the meetings, including the appointment of local committees.

Sec. 3. Whenever the proper officers of a number of related societies shall have a conference covering matters of mutual interest to the several societies, he shall act as the delegate or representative of this Society.

Sec. 4. He shall make such purchases and employ such assistance as will, in his judgment, expedite the business of the Society, and

Sec. 5. He shall be reimbursed out of the funds of the Society for expenses incurred in attending meetings of the Society.

ARTICLE V

TREASURER

Section 1. The Treasurer shall be in charge of the funds of the Society.

Sec. 2. At the annual business meeting of the Society he shall present a statement to date of the funds of the Society.

Sec. 3. He shall make such purchases and employ such assistance as will, in his judgment, expedite the business of the Society.

ARTICLE VI

AUDITING COMMITTEE

The President shall annually appoint an auditing committee of two, who shall audit and report upon the financial record and statement of the Treasurer at the meeting for which they were appointed.

ARTICLE VII

PROGRAM RULES

In matters relating to programs for annual meetings, the following rules shall be observed:

Section 1. Titles and abstracts of papers to be presented by any method at the annual meeting must be sent to the Secretary in duplicate before the final date set by him. The length, form, and arrangement of the abstracts must comply with the requests of the Secretary in order to insure prompt publication by The Wistar Institute. The titles and abstracts of papers which do not conform to such requests or papers which are received late may be presented by title only.

Sec. 2. Titles shall be listed in groups according to subject matter, the groups to be determined by the Secretary.

Sec. 3. Whenever conditions require, the Secretary shall schedule two or more groups for the same hour and arrange the program to bring together papers on subjects of more general interest for meetings of the whole Society.

Sec. 4. Each member may have not more than fifteen minutes of the time of the Society at the annual meeting. This time may be used by him to present one or more papers personally or to introduce papers of non-members.

Sec. 5. All papers not read when called for as listed shall be placed at the end of the group list, and if not read when called for the second time, shall be read by title only.

Sec. 6. The titles of "introduced" papers may be listed in the groups after the titles of papers to be read by members.

LIFE AND ACTIVE MEMBERS

(* indicates life members of the Society; † indicates charter members of the American Morphological Society; mail addresses are in italics.)

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Totals

Life members	7
Active members	1039
Associate members	377
Grand total	1423

INDEX

- A** DRENAL glands after repeated injections of histamine in albino mice, histological studies of the . . . 227
- Adrenalectomized female mice, the relative growth of the mammary glands in normal, ovariectomized and . . . 279
- AMERICAN SOCIETY OF ZOOLOGISTS. Proceedings of the fifty-second annual meeting, Michigan State University, East Lansing, Michigan, September 6, 7, 8, 1955. Constitution, by-laws and list of members . . . 531
- Amphibian development, inhibitors of Amniotic fluid of the mouse, a physiological study of the. I. Volume and weight changes of the amniotic fluid compared with the weights of fetus and placenta during gestation . . . 359
- Anatomic-physiologic study, an. Effect of vagus nerves on heart rate of young dogs: . . . 521
- Anatomy of the genital system and two endocrine organs and body weights in the chinchilla, some observations on the gross . . . 201
- Anomalous colon, a case of left-sided vermiform appendix, cecum and . . . 301
- Application of a freezing-substitution method of fixation to tissue culture preparations, the . . . 1
- Arteries, an unusual variation in origin of the hepatic and splenic . . . 335
- Ash weight of human skeletons in percent of their dry, fat-free weight . . . 341
- Axon terminals in the normal human cerebrum and cerebellum . . . 239
- Azo dyes chemically related to trypan blue, teratogenic activity of several . . . 313
- B** ENSLEY, SYLVIA H. See Stevens, Patricia F. . . . 227
- Body growth and compared with the metanephroi of other species, the development of the hamster metanephros correlated with general . . . 259
- Body weights in adults of small sized race X, organ size in relation to. XII. Morphogenetic studies of the rabbit . . . 81
- Bufo americanus, hormonal influences on sex differentiation in the toad . . . 467
- C** ARDIOINHIBITORY branches of the right vagus nerve in the dog, isolation of the . . . 437
- Cat, rabbit, guinea pig and rat, nerve fibers in the area postrema of . . . 65
- Cecal villi in *Dicrostonyx torquatus* (Rodentia: Microtinae) . . . 125
- Cecum and anomalous colon, a case of left-sided vermiform appendix . . . 291
- Celiac and mesenteric plexuses, components of periarterial extensions of . . . 509
- Cells of the seminiferous tubules, volume changes in the. III. Quantitative studies on spermatogenesis in the albino rat . . . 385
- Cerebellum, axon terminals in the normal human cerebrum and . . . 239
- Cerebrum and cerebellum, axon terminals in the normal human . . . 239
- CHANG, CHIH YU. Hormonal influences on sex differentiation in the toad, *Bufo americanus* . . . 467
- Changes of the amniotic fluid compared with the weights of fetus and placenta during gestation, volume and weight. I. A physiological study of the amniotic fluid of the mouse . . . 521
- Chick embryos, regeneration in the hindbrain of neural tube stages of . . . 169
- Chinchilla, some observations on the gross anatomy of the genital system and two endocrine organs and body weights in the . . . 301
- CLAUSEN, H. J. An unusual variation in origin of the hepatic and splenic arteries . . . 335
- CLEMENTE, C. D., AND V. L. VAN BREEMEN. Nerve fibers in the area postrema of cat, rabbit, guinea pig and rat . . . 65
- COOPER, W. GREGORY. Succinic dehydrogenase activity in the prenatal and post-natal rat heart . . . 103
- Cyclic changes in the thyroid and interrenal glands of the viviparous lizard, *Xantusia vigilis* . . . 19
- D** ECAPITATION in the rat, a method for fetal hypophysectomy by . . . 183
- DEITCH, ARLINE D., AND GABRIEL C. GODMAN. The application of a freezing-substitution method of fixation to tissue culture preparations . . . 1
- DEMPSEY, EDWARD W. See Wislocki, George B. . . . 33
- DEMPSEY, EDWARD W. See Wislocki, George B. . . . 133
- Dicrostonyx torquatus* (Rodentia: Microtinae), cecal villi in . . . 125
- Dog, isolation of the cardioinhibitory branches of the right vagus nerve in the . . . 437
- Dogs, effect of vagus nerves on heart rate of young: An anatomic-physiologic study . . . 201
- DOMM, L. V., AND PIERRE LEROY. A method for fetal hypophysectomy by decapitation in the rat . . . 183

- Dry, fat-free weight, ash weight of human skeletons in per cent of their 341
- Dwarf gene upon organ size and variability in race X, the influence of the. XIII. Morphogenetic studies of the rabbit 447
- E**LECTRON microscopy of the human placenta 133
- Electron microscopy of the placenta of the rat 33
- Endocrine organs and body weights in the chinchilla, some observations on the gross anatomy of the genital system and two 301
- ENGELMAN, MORRIS. See Liedke, Kathe B. 359
- F**AT-FREE weight, ash weight of human skeletons in per cent of their dry 341
- Fetal hypophysectomy by decapitation in the rat, a method for 183
- Fetus and placenta during gestation, volume and weight changes of the amniotic fluid compared with the weights of. I. A physiological study of the amniotic fluid of the mouse 521
- Freezing-substitution method of fixation to tissue culture preparations, the application of a 1
- G**ANGLIA, the fine structure of young and old spinal 399
- Genital system and two endocrine organs and body weights in the chinchilla, some observations on the gross anatomy of the 301
- Gestation, volume and weight changes of the amniotic fluid compared with the weights of fetus and placenta during. I. A physiological study of the amniotic fluid of the mouse 521
- GIBSON, W. C., J. R. SMYTHIES, V. A. PURKIS AND G. E. MORRISON, JR. Axon terminals in the normal human cerebrum and cerebellum 239
- GODMAN, GABRIEL C. See Deitch, Arline D. 1
- GORDON, ALBERT SAUL. See Phillips, Joy Burcham 487
- GRAFF, SAMUEL. See Liedke, Kathe B. 359
- Guinea pig and rat, nerve fibers in the area postrema of cat, rabbit 65
- H**ALPERN, MYRON H. The sino-atrial node of the rat heart 425
- Hamster metanephros correlated with general body growth and compared with the metanephroi of other species, the development of the 259
- Heart rate of young dogs, effect of vagus nerves on: An anatomic-physiologic study 201
- Heart, succinic dehydrogenase activity in the pre-natal and post-natal rat 103
- Heart, the sino-atrial node of the rat 425
- Hepatic and splenic arteries, an unusual variation in origin of the 335
- HESS, ARTHUR. The fine structure of young and old spinal ganglia 399
- Hindbrain of neural tube stages of chick embryos, regeneration in the 169
- Histamine in albino mice, histological studies of the adrenal glands after repeated injections of 227
- Histological studies of the adrenal glands after repeated injections of histamine in albino mice 227
- Hormonal influences on sex differentiation in the toad, *Bufo americanus* 467
- Human cerebrum and cerebellum, axon terminals in the normal 239
- Human placenta, electron microscopy of the 133
- Human skeletons in per cent of their dry, fat-free weight, ash weight of 341
- I**MMATURE rats, a study of pituitary-thyroid relations in 487
- Influence of the dwarf gene upon organ size and variability in race X, the. XIII. Morphogenetic studies of the rabbit 447
- Inhibitors of amphibian development 359
- Interrenal glands of the viviparous lizard, *Xantusia vigilis*, cyclic changes in the thyroid and 19
- Isolation of the cardioinhibitory branches of the right vagus nerve in the dog 437
- J**ACOBS, MERLE W. See Kuntz, Albert 509
- K**ALLEN, BENGT. Regeneration in the hindbrain of neural tube stages of chick embryos 169
- KUNTZ, ALBERT, AND MERLE W. JACOBS. Components of periaortic extensions of celiac and mesenteric plexuses 509
- L**ATIMER, HOMER B., AND PAUL B. SAWIN. Morphogenetic studies of the rabbit. XII. Organ size in relation to body weights in adults of small sized race X 81
- LATIMER, HOMER B., AND PAUL B. SAWIN. Morphogenetic studies of the rabbit. XIII. The influence of the dwarf gene upon organ size and variability in race X 447
- LEROY, PIERRE. See Domm, L. V. 183
- LIEDKE, KATHE B., MORRIS ENGELMAN AND SAMUEL GRAFF. Inhibitors of amphibian development 359
- Lizard, *Xantusia vigilis*, cyclic changes in the thyroid and interrenal glands of the viviparous 19
- LONG, D. M. See Truex, R. C. 201
- M**CCAFFERTY, ROBERT E. A physiological study of the amniotic fluid of the mouse. I. Volume and weight changes of the amniotic fluid compared with the weights of fetus and placenta during gestation 521
- Mammary glands in normal, ovariectomized female mice, the relative growth of the 279
- Mesenteric plexuses, components of periaortic extensions of celiac and 509
- Metanephroi of other species, the development of the hamster metanephros correlated with general body growth and compared with the 259

Mice, histological studies of the adrenal glands after repeated injections of histamine in albino	227	Placenta, electron microscopy of the human	133
Mice, the relative growth of the mammary glands in normal, ovariectomized and adrenalectomized female	279	Placenta of the rat, electron microscopy of the	33
MILLER, MALCOLM R. Cyclic changes in the thyroid and interrenal glands of the viviparous lizard, <i>Xantusia vigilis</i>	19	Plexuses, components of periarterial extensions of celiac and mesenteric	509
MIZERES, NICHOLAS JAMES. Isolation of the cardioinhibitory branches of the right vagus nerve in the dog	437	Post-natal rat heart, succinic dehydrogenase activity in the pre-natal and	103
Morphogenetic studies of the rabbit. XII. Organ size in relation to body weights in adults of small sized race X	81	Postrema of cat, rabbit, guinea pig and rat, nerve fibers in the area	65
Morphogenetic studies of the rabbit. XIII. The influence of the dwarf gene upon organ size and variability in race X	447	Pre-natal and post-natal rat heart, succinic dehydrogenase activity in the	103
MORRISON, G. E., JR. See Gibson, W. C.	239	PURKIS, V. A. See Gibson, W. C.	239
Mouse, a physiological study of the amniotic fluid of the. I. Volume and weight changes of the amniotic fluid compared with the weights of fetus and placenta during gestation	521	Q UANTITATIVE studies on spermatogenesis in the albino rat. III. Volume changes in the cells of the seminiferous tubules	385
N ERVE fibers in the area postrema of cat, rabbit, guinea pig and rat	65	R ABBIT, guinea pig and rat, nerve fibers in the area postrema of cat	65
Neural tube stages of chick embryos, regeneration in the hindbrain of	169	Rabbit, morphogenetic studies of the. XII. Organ size in relation to body weights in adults of small sized race X	81
Node of the rat heart, the sino-atrial	425	Rabbit, morphogenetic studies of the. XIII. The influence of the dwarf gene upon organ size and variability in race X	447
Normal, ovariectomized and adrenalectomized female mice, the relative growth of the mammary glands in	279	Race X, organ size in relation to body weights in adults of small sized. XII. Morphogenetic studies of the rabbit	81
O RGAN size and variability in race X, the influence of the dwarf gene upon. XIII. Morphogenetic studies of the rabbit	447	Race X, the influence of the dwarf gene upon organ size and variability in. XIII. Morphogenetic studies of the rabbit	447
Organ size in relation to body weights in adults of small sized race X. XII. Morphogenetic studies of the rabbit	81	RAMM, GORDON M., AND GORDON E. SWARTZ. The development of the hamster metanephros correlated with general body growth and compared with the metanephroi of other species	259
Origin of the hepatic and splenic arteries, an unusual variation in	335	Rat, a method for fetal hypophysectomy by decapitation in the	183
Ovariectomized and adrenalectomized female mice, the relative growth of the mammary glands in normal	279	Rat, electron microscopy of the placenta of the	33
P ERIARTERIAL extensions of celiac and mesenteric plexuses, components of	509	Rat heart, succinic dehydrogenase activity in the pre-natal and post-natal	103
PETERSON, ROY R. See Trotter, Mildred	341	Rat heart, the sino-atrial node of the	425
PHILLIPS, JOY BURCHAM, AND ALBERT SAUL GORDON. A study of pituitary-thyroid relations in immature rats	487	Rat, nerve fibers in the area postrema of cat, rabbit, guinea pig and	65
Physiological study of the amniotic fluid of the mouse, a. I. Volume and weight changes of the amniotic fluid compared with the weights of fetus and placenta during gestation	521	Rat, quantitative studies on spermatogenesis in the albino. III. Volume changes in the cells of the seminiferous tubules	385
Pituitary-thyroid relations in immature rats, a study of	487	Rats, a study of pituitary-thyroid relations in immature	487
Placenta during gestation, volume and weight changes of the amniotic fluid compared with the weights of fetus and. I. A physiological study of the amniotic fluid of the mouse	521	RICHARDSON, FLAVIA L. The relative growth of the mammary glands in normal, ovariectomized and adrenalectomized female mice	279
		(Rodentia: Microtinae), cecal villi in <i>Dicrostonyx torquatus</i>	125
		ROOS, THOMAS B., AND RICHARD M. SHACKELFORD. Some observations on the gross anatomy of the genital system and two endocrine organs and body weights in the chinchilla	301
		ROOSEN-RUNGE, EDWARD C. Quantitative studies on spermatogenesis in the albino rat. III. Volume changes in the cells of the seminiferous tubules	385

- S**AWIN, PAUL B. See Latimer, Homer B. 81
- S**AWIN, PAUL B. See Latimer, Homer B. 447
- S**COTT, J. C. See Truex, R. C. 201
- Seminiferous tubules, volume changes in the cells of the. III. Quantitative studies on spermatogenesis in the albino rat 385
- Sino-atrial node of the rat heart, the 425
- Sex differentiation in the toad, *Bufo americanus*, hormonal influences on 467
- S**HACKELFORD, RICHARD M. See Roos, Thomas B. 301
- S**MYTHE, M. Q. See Truex, R. C. 201
- S**MYTHIES, J. R. See Gibson, W. C. 239
- Species, the development of the hamster metanephros correlated with general body growth and compared with the metanephroi of other 259
- Spermatogenesis in the albino rat, quantitative studies on. III. Volume changes in the cells of the seminiferous tubules 385
- Spinal ganglia, the fine structure of young and old 399
- Splenic arteries, an unusual variation in origin of the hepatic and 335
- S**TEVENS, PATRICIA F., AND **S**YLVIA H. BENSLEY. Histological studies of the adrenal glands after repeated injections of histamine in albino mice 227
- Structure of young and old spinal ganglia, the fine 399
- Succinic dehydrogenase activity in the pre-natal and post-natal rat heart 103
- S**WARTZ, GORDON E. See Ramm, Gordon M. 259
- T**ERATOGENIC activity of several azo dyes chemically related to trypan blue 313
- Thyroid and interrenal glands of the viviparous lizard, *Xantusia vigilis*, cyclic changes in the 19
- Tissue culture preparations, the application of a freezing-substitution method of fixation to 1
- Toad, *Bufo americanus*, hormonal influences on sex differentiation in the 467
- T**ROTTER, MILDRED, AND **R**OY R. PETERSON. Ash weight of human skeletons in per cent of their dry, fat-free weight 341
- T**RUEX, R. C., J. C. **S**COTT, D. M. LONG AND M. Q. **S**MYTHE. Effect of vagus nerves on heart rate of young dogs: An anatomic-physiologic study 201
- Trypan blue, teratogenic activity of several azo dyes chemically related to 313
- V**AN BREEMEN, V. L. See Clemente, C. D. 65
- Vagus nerve in the dog, isolation of the cardioinhibitory branches of the right 437
- Vagus nerves on heart rate of young dogs, effect of: An anatomic-physiologic study 201
- Vermiform appendix, cecum and anomalous colon, a case of left-sided 291
- V**OGE, MARIETTA, AND **H**OWARD A. BERN. Cecal villi in *Dicrostonyx torquatus* (Rodentia: Microtinae) 125
- Volume changes in the cells of the seminiferous tubules. III. Quantitative studies on spermatogenesis in the albino rat 385
- W**ILSON, JAMES G. Teratogenic activity of several azo dyes chemically related to trypan blue 313
- W**ISLOCKI, GEORGE B., AND **E**DWARD W. DEMPSEY. Electron microscopy of the placenta of the rat 33
- W**ISLOCKI, GEORGE B., AND **E**DWARD W. DEMPSEY. Electron microscopy of the human placenta 133
- W**RIGHT, CLARENCE W. A case of left-sided vermiform appendix, cecum and anomalous colon 291
- X**ANTUSIA *vigilis*, cyclic changes in the thyroid and interrenal glands of the viviparous lizard 19

